Title: Thinking locally: Environmental reconstruction of Middle and Later Stone Age archaeological sites in Ethiopia, Kenya, and Zambia based on ungulate stable isotopes

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Abstract

Our knowledge of the Pleistocene environments of Africa consists primarily of data at a scale too coarse to capture the full habitat variation important to hominins ‘on the ground.’ These environments are complex, highly variable, and poorly understood. As such, data from individual sites are a needed addition to our current paleoenvironmental reconstructions. This study offers a site-based approach focusing on stable isotope analyses of fossil faunal tooth enamel from three archaeological sites in tropical Africa. Carbon and oxygen stable isotope data are reported from the sites of Porc Epic, Ethiopia, Lukenya Hill, Kenya, and Kalembo Rockshelter, Zambia. Stable isotope data from tooth enamel are used to measure two environmental variables: (1) aridity based on oxygen isotope composition and (2) dietary reconstructions of fossil ungulates based on the relative proportions of C₃ browse and C₄ graze in the diet. These data allow for a preliminary assessment of existing models that attempt to explain the behavioral and technological variation characteristic of the transition between the Middle and Later Stone Ages. Results indicate spatial and temporal variation in aridity and phytogeography in tropical Africa during the Pleistocene, suggesting that no single model is likely to provide an explanation for the transition at all sites across Africa.

Keywords: herbivore isotope analysis; Late Pleistocene; human behavior; Porc Epic; Lukenya Hill; Kalembo Rockshelter

Introduction

Social, demographic, and behavioral transitions during the Late Pleistocene (~126–12 ka) in Africa are critical events in human evolution. The Late Pleistocene is characterized by archaeological diversity, including sudden behavioral changes, reversals of those changes, and sometimes returns to previous states (Ambrose and Lorenz, 1990; McBrearty and Brooks, 2000; Henshilwood and Marean, 2003; Marean and Assefa, 2005; d’Errico and Stringer, 2011; Wurz, 2013; Tryon and Faith, 2013). Technological traditions and indicators of behavior develop from the Middle to the Later Stone Age (MSA and LSA, respectively) between ~60 ka and 20 ka, embedded within an oscillating climate dominated by humid/arid cycling (Barham, 2000; Basell, 2008; Chase, 2010; Blome et al., 2012; Scerri, 2013; Tryon and Faith, 2013, 2016; Tryon et al., 2014; Trauth et al., 2015; Robinson et al., 2016). The transition from the MSA to the LSA is asynchronous across Africa, perhaps occurring around or earlier than 50 ka at some sites in East and South Africa (Beaumont et al., 1978; Ambrose 1998a, 2002; Grun and Beaumont, 2001; Diez-Martin et al., 2009; Tryon and Faith, 2016), but not until after 25 ka at others (Clark, 1997; Marean et al., 2014). Understanding why there was a MSA–LSA transition is a major goal of modern Stone Age archaeology (Barham and Mitchell, 2008; Tryon and Faith, 2013, 2016; Wurz, 2013). It is likely that the behavioral and technological changes that accompanied the MSA to LSA transition were related to a combination of changes in human cognition (Klein, 2009), environmental conditions (Ambrose, 1998a, b; Chase and Meadows, 2007; Chase, 2010; Blome et al., 2012), and demographic factors (Powell et al., 2009; d’Errico and Stringer, 2011; Mackay et al., 2014). The dynamics between these factors may have varied in different parts of Africa. Development and testing of these models, however, are inhibited by a lack of site-specific paleoenvironmental data and a record of local climatic conditions and environmental

patterns during the Pleistocene.

The MSA/LSA Transition

A concise definition of what constitutes the transition from the MSA to the LSA is difficult to articulate. Changes in the production and sourcing of stone tools and the use and manufacture of material for personal adornment may elucidate the differences in social networks between the MSA and the LSA (Merrick et al., 1994; Ambrose, 2002; d’Errico et al., 2012; Tryon and Faith, 2013, 2016). Stone tool technology remains the most common feature of archaeological assemblages during this time and is often used to help to delineate between the MSA and the LSA. As Ambrose (1998a, 2002) thoroughly discusses, however, there is no simple set of characters that signals a universal transition. Microlithization and backed blade-based technology are often considered the hallmarks of the LSA (Ambrose 1998b; McBrearty and Brooks, 2000; Diez-Martin et al., 2009). It is notable, though, that blade-based technology appears ~500 ka in both the Kapthurin Formation of Kenya (Johnson and McBrearty, 2010) and at Kathu Pan in South Africa (Wilkins et al., 2012), although these are not backed-blades. Furthermore, the Howiesons Poort of South Africa is a microlithic industry with backed-pieces that dates to between ~70 ka and ~60 ka and is considered MSA since there appears to be a reversion to larger, non-microlithic tools sometime after ~60 ka (Jacobs et al., 2008; Henshilwood et al., 2014). Some LSA sites, like Shum Laka (Cornelissen, 1996, 2003), are not characterized by blade-based assemblages and have very few backed pieces. Despite these regional – even site-to-site – differences, most researchers agree that the abandonment of Levallois core reduction and the increase of microlithization signifies the beginning of the LSA in East Africa ~55-40 ka (Ambrose, 1998b, 2002; Tryon and Faith, 2013), and that the use of

bipolar cores at Border Cave ~44 ka signifies the beginning of the LSA in South Africa which culminated in the bladelet dominated Robberg Industry sometime around ~22 ka (Villa et al., 2012; Marean et al., 2014).

Various environmental and non-environmental hypotheses, often not mutually exclusive, have been proposed to explain the transition from the MSA to the LSA. Ambrose (1998a, b, 2002) offers a scenario where the combination of more arid and/or less predictable environments and increased social connectivity and information exchange was a catalyst for the LSA.

Following the hypothesis that inter-group reciprocity serves to reduce risk in unpredictable environments (Deacon, 1992, 1995; Deacon and Wurz, 1996; Wurz, 1997; Fitzhugh, 2001), Ambrose (2002) demonstrates that the earliest indicators of the LSA coincide with increased frequencies of nonlocal, fine-grained lithic material during a time of cooler and drier conditions ~60 ka to ~55 ka, especially in East Africa. The sharing of these 'exotic' materials may have facilitated trade and information networks during this arid climate interval. Knowledge of nonlocal environmental conditions and faunal migratory patterns may have allowed for the development of specialized LSA toolkits, as opposed to the more generalized toolkits of the MSA. Further microlithization might have been a response to reduced trade in nonlocal lithic raw materials related to the rise in the use of ostrich eggshell (OES) and other aspects of personal adornment to indicate social partnerships (Ambrose and Lorenz, 1990; Ambrose, 1998a, 2002).

Eren et al. (2013), working with material from Mumba Rockshelter in Tanzania, suggest that climate amelioration combined with demographic change leading to increased territoriality offers an explanation for the origins of the LSA. They define climate amelioration as locally more mesic conditions as evidenced in the Lake Malawi core (Scholz et al., 2011), and assume increasing population size based on site density (e.g., Blome et al., 2012). Eren et al. (2013)

argue that the technological changes leading to the LSA were a result of territorial and resource defense, as opposed to the creation of extra-local social networks. With a large, attractive, resource-abundant area to defend, there would have been increased time constraints and subsistence risks with migratory prey. These constraints and risks may have been minimized by the more portable, maintainable, and reliable aspects of LSA toolkits, including bipolar core technology (Nelson, 1991; Hiscock et al., 2011; Eren et al., 2013). If the origins of the LSA are related to more mesic environments and greater territoriality, Phillipson's (1980) proposal that backed-microliths were used as stone inserts for arrowheads for hunting in dense vegetation could be resurrected. In fact, the idea that microliths (although not true-LSA microliths) were used as arrowheads was experimentally tested with the Howiesons Poort assemblage from Sibudu Cave (Lombard and Phillipson, 2010).

Recently, Tryon and Faith (2016) proposed a model for the transition from the MSA to the LSA which they say 'crosscuts' indicators of habitat change. Their evidence from Nasera Rockshelter in Tanzania suggests a combination of reduced residential mobility due to increased population density and more intensive exploitation of the immediate local landscape. Nonlocal raw material is abundant in the Levallois dominated MSA assemblages, but actually becomes less common in the transitional MSA-LSA Nasera Industry (~37-25 ka) which they argue characterizes a less residentially mobile and more territorial population. With increased time and subsistence costs related to greater territoriality, as in the model proposed by Eren et al. (2013), portable and reliable backed-microliths would have kept risk low (Nelson, 1991; Fitzhugh, 2001; Bousman, 2005). Since this lithic pattern continues through the LSA Lemuta Industry during the Last Glacial Maximum and into the more mesic and humid early Holocene, they propose that the LSA is a result of increased population pressure unrelated, or minimally related, to

environmental change (Tryon and Faith, 2016).

The purpose of the stable isotope analysis presented here is not to offer a new model of the potential relationship between climate change, the MSA-LSA transition, and demography, nor is it to rigorously test the above models. Just as the timing of the transition is asynchronous across Africa, and the types of artifacts which signal the transition differ from site-to-site, it is likely that the exact climatic and demographic aspects of the transition were also not universal. It is possible that each of the above models, or at least aspects of each, played out during the MSA-LSA transition at a specific site or region of Africa. Instead, the current stable isotope study is intended to provide local climatic and environmental data from Late Pleistocene archaeological sites which are sorely missing from the above hypotheses and other recent syntheses (e.g., Blome et al., 2012; Conard and Will, 2015). New faunal enamel isotopic data are presented here from three sites – Porc Epic, Ethiopia, Lukenya Hill, Kenya, and Kalemba Rockshelter, Zambia (Table 1; Figure 1). An understanding of the climatic and environmental contexts and trends at these sites allows for an evaluation and refinement of MSA-LSA transition models.

Chronology and Archaeology of the Study Sites

The use of herbivore faunal tooth enamel as a proxy for site-specific environmental and climatic conditions offers a more locally nuanced investigation of variation than is possible with soil carbonates or core records. While soil carbonates also provide a measure of site-specific conditions, they are spatially restricted records ($\sim 10 \text{ m}^2$) and typically provide a signal averaged over thousands or tens of thousands of years (Kingston et al., 1994; Uno et al., 2016). Enamel carbonates provide comparatively short temporal signals, in the order of months during mineralization, and potentially a much larger spatial signal related to the foraging and migratory

radii of large ungulates (Kingston, 2007). Furthermore, as these sites are rockshelters and caves, there are no paleosols available for soil carbonate analysis. Each of the study sites was systematically excavated, contain diverse faunal assemblages, including hominin remains, and span behaviorally relevant transitions during the Late Pleistocene. Chronological and archaeological information for each site is described in turn below and summarized in Table 1.

Porc Epic Cave

Porc Epic Cave is located between the Afar Depression and the Somali Plateau in the Dire Dawa region of eastern Ethiopia at ~140 m above the wadi Laga Dachatu (Figure 1). Despite the wadi below, the environment today is quite dry, receiving ~600 mm of precipitation during two rainy seasons supporting an acacia and scrub-dominated vegetation. Average temperatures in Dire Dawa are ~24° with a range of ~7°C (Ingersol, 1968; Wolde-Mariam 1972; Assefa, 2006; Assefa et al., 2014; Rosso et al., 2014; IAEA/WMO, 2016). The site was discovered by Teilhard de Chardin (1930) and excavated in 1933 by Henri Breuil and Paul Wernert (Teilhard de Chardin et al., 1940), but much of this material and contextual information have been lost and are not considered further here. Instead, this study considers the ~49 m² excavated by Clark and Williamson from 1974–1976 (Clark and Williamson, 1984). Following the stratigraphic section developed by Clark and Williamson (1984), Pleurdeau (2001, 2003, 2005) recognized four main stratigraphic units. Three of these are of assumed Pleistocene age and are considered MSA. The fourth is a thin Holocene LSA layer. This fourth unit is separated from the MSA units by a pronounced unconformity and a flowstone (Pleurdeau, 2001, 2005). It is not considered in this study.

Chronology Several attempts at developing a chronology for Porc Epic Cave have been made

since the 1974–1976 excavations. Ionium dating and conventional ^{14}C radiocarbon dating were performed on the flowstone with the aim to produce a minimum age for the MSA units. These samples provided dates of 4590 ± 60 years BP (before present) for radiocarbon and 6270 ± 1020 years BP for the Ionium method (Clark and Williamson, 1984). Clark and Williamson (1984) note that the dates may be inaccurate due to carbonate dilution, detrital Thorium-232, and/or the fact that the dripstone may have been formed much later than the MSA occupation. In any case, these dates are too young to provide a minimum age for the MSA at Porc Epic. Michels and Marean (1984) performed hydration dating on three MSA obsidian artifacts from the 1933 excavation. While there was no associated stratigraphic information with any of the obsidian artifacts, the average of three samples from each artifact provided dates of $61,202 \pm 958$ years BP (Artifact 12022), $61,640 \pm 1083$ years BP (Artifact 12018), and $77,565 \pm 1575$ years BP (Artifact 12020). Assuming that the Porc Epic assemblage was deposited during a glacial period, and that the temperature was cooler than at present, these dates are minimum estimates, perhaps by as many as 20,000 years (Michels and Marean, 1984). More recently, accelerator mass spectrometry (AMS) ^{14}C analysis was performed on gastropod shells found at 160–170 cm, 180–190 cm, and 270–280 cm below the surface (cmbs). These samples yielded ages of $33,700 \pm 300$ calibrated (cal) years BP, $35,600 \pm 350$ calibrated years BP, and $> 43,200$ calibrated years BP (Assefa, 2006). It is known, however, that gastropods incorporate ingested calcium carbonate into their shells, leading to anomalous radiocarbon dates (Goodfriend, 1987). As such, the gastropod dates are minimum dates and probably less reliable than the obsidian hydration dates.

Archaeology Clark and Williamson (1984) interpreted the spatial distribution and density of the artifacts at the site to suggest that Porc Epic Cave was repeatedly occupied in brief episodes over several millennia. This analysis is supported by the ~16,000 year spread in obsidian hydration

dates which would correlate with an exceeding slow sedimentary accumulation for the site (Michel and Marean, 1984). While there appear to be at least four, and possibly more, distinct stratigraphic levels at Porc Epic (Clark and Williamson, 1984; Pleurdeau, 2001; Leplongeon, 2014; Rosso et al., 2014), both the lithic (Pleurdeau, 2003, 2005) and faunal remains (Assefa, 2002, 2006) have previously been analyzed as one continuous unit. However, the evidence suggests multiple brief – and perhaps seasonal – occupations. In fact, based on a recent study of the use and manufacture of ochre artifacts at the site (Rosso et al., 2014), material from 60–160 cmbs appears to date to a distinctly later period from the assemblage located at 160–300 cmbs. In the analysis of the stone tool artifacts, Pleurdeau (2001, 2003, 2005) suggests a gradual evolution in the three Pleistocene units from the MSA to the earliest LSA, with microliths and backed bladelets mixed in with Levallois flakes and points, but no clear clustering of artifacts, obvious vertical breaks, or typo-technological variations in the sequence.

The faunal assemblage includes a significant number of historically absent alcelaphines and reduncines. Reduncines are more common earlier in the sequence with alcelaphines becoming more common in and above the 160 cmbs level (Assefa 2006). Reduncines are indicators of seasonally wet grasslands while alcelaphines are typically associated with dry grasslands. This shift from an assemblage dominated by reduncines to one dominated by alcelaphines corroborates the interpretations of Clark and Williamson (1984) of the environment of Porc Epic becoming more arid over time. Assefa (2002, 2006) suggests that the site may have been on an ecotone during the Late Pleistocene due to its location on the edge of the Rift Valley. This location would have provided occupants with the ability to monitor and track faunal migration in the rift as well as on nearby ridges, offering them access to an altitudinal gradient of ecological zones (Clark and Williamson, 1984; Assefa, 2006). It is also of note that Assefa

(2002) identifies both the modern African buffalo (*Syncerus caffer*) and the extinct giant long-horn buffalo (*Syncerus antiquus*) in the Porc Epic assemblage. The lack of horn cores or other direct morphological indicators make confirmation of assignment to *S. antiquus* difficult to assess, but the length of the two M3s sampled here – 48.04 mm and 46.61 mm – are well above the average M3 length for extant *S. caffer* (37.28 mm) and similar to the mean for *S. antiquus* (50.95 mm) from Elandsfontein reported by Klein (1994). As such, Assefa's original (2002) identifications are preserved in the current study, even though he later argued (Assefa, 2006) that no extinct species were sampled at Porc Epic. Finally, fragmentary human remains were recovered during the original excavations in 1933 from the MSA sequence (Vallois, 1951).

Lukenya Hill

Lukenya Hill is a ~16 km² gneissic inselberg in southern Kenya rising above the Athi-Kapiti Plains in a semi-arid acacia bushland environment (Figure 1) which averages ~25°C and receives ~500 mm of precipitation per year in two irregular rainy seasons (White, 1983; Marean, 1990, 1992; Barut, 1994, 1997; Kusimba, 2001). Mary and Louis Leakey carried out the first work at Lukenya Hill in the 1940s at a Neolithic aged site (GvJm2). No formal reports have been published on these excavations, except Gramly's description of them as a field school for amateur archaeologists (Gramly, 1975, 1976). Nearly 300 other Lukenya Hill sites, ranging from the Acheulian through the Iron Age, have since been discovered (Marean, 1990; Kusimba, 2001; Kusimba and Kusimba, 2003). Four of the Pleistocene aged Lukenya Hill sites – GvJm-22, GvJm-62, GvJm-19, and GvJm-46 – are considered in this study. GvJm-22 is a rockshelter which was discovered and excavated by Gramly in 1970–1971. Conventional radiocarbon dates on charcoal and bone collagen, and detailed analysis of the stone tool artifacts, suggested both

Holocene and Pleistocene occupations (Gramly, 1976; Barut, 1997; Kusimba, 2001). The Holocene units include Pastoral Neolithic and LSA assemblages while the Pleistocene at GvJm-22 is characterized by LSA and MSA artifacts (Gramly, 1975, 1976; Marean, 1990, 1992; Kusimba, 2001; Tryon et al., 2015). Only the Pleistocene material is included in this study. GvJm-62 and GvJm-19 were excavated as part of a large-scale University of Massachusetts survey and excavation project led by John Bower and Charles Nelson (Bower et al., 1977; Bower and Nelson, 1978; Marean, 1990). GvJm-62 is an open-air site discovered by Stanley Ambrose in 1978 and excavated from 1978-1981 by the Bower-Nelson group. It is also described as having two main archaeological units, one Holocene LSA and one Pleistocene LSA (Marean, 1990, 1992; Marean and Gifford-Gonzalez, 1991). Isotope data on the Pleistocene LSA fauna from the Bower-Nelson excavation is included in this study. Fauna from Kusimba's excavation of GvJm-62 in 1994 was not sampled for this study. GvJm-19 is a rock overhang located just north of GvJm-22, excavated from 1978-1980 by the Bower-Nelson group. Conventional radiocarbon dates indicated three archaeological units dating from the terminal Pleistocene through the early-mid Holocene (Nelson and Kimengich, 1984; Marean, 1990, Kusimba, 2001). Only material from the terminal Pleistocene assemblage, attributed to the LSA, is considered in this study. GvJm-46 is an open-air site which was excavated in 1977–1978 and 1981 by a team led by Sheryl Miller. Two separate Pleistocene assemblages were recovered from GvJm-46, both described as LSA by Miller (1979). While there are slight differences between the assemblages, Miller (1979) hesitated to call the older assemblage MSA, but Marean (1990) quotes Nelson and Merrick as describing it as late MSA. The small sample size of dentition from the LSA unit (Marean, 1990) restricted sampling in this study to the older MSA assemblage.

Chronology Only material which can confidently be placed in the Pleistocene at each of the four Lukenya Hill sites has been sampled for this study. Of the four sites, GvJm-22 is the only one which has had its chronology rigorously reassessed. Gramly's excavation (Gramly, 1975, 1976; Gramly and Rightmire, 1973) included three trenches (A, B, and C) and a test pit. Material from a sediment balk in trench C is indicated with the designation C+ balk. Gramly (1975, 1976) reported eight conventional radiocarbon dates on bone collagen from the C+ balk unit. The dates revealed four Holocene Pastoral Neolithic and LSA occurrences (A–D; 0–110 cmbs) dated to between 1234 ± 104 cal BP and 2245 ± 62 cal BP, and two Pleistocene occurrences, E (120–150 cmbs), with dates of $21,461 \pm 977$ cal BP and $21,483 \pm 926$ cal BP, and F (170–205 cmbs), dated to between $11,487 \pm 482$ cal BP and $18,609 \pm 520$ cal BP (calibrated dates from Tryon et al., 2015). Recently, Tryon et al. (2015) re-dated the GvJm-22 sequence using AMS ^{14}C analysis of unmodified OES. Gramly's stratigraphically inverted dates for occurrences E and F, and the unreliable nature of collagen and apatite dates on bone from the tropics (Marean, 1990; Higham et al., 2006), made the original dates suspect. Even with the new dates, Tryon et al. (2015) identified a number of stratigraphic inconsistencies, including the fact that the ages of occurrences E and F differ among the excavation trenches and the test pit. In trench A, occurrence E dates to between $15,193 \pm 100$ cal BP and $21,884 \pm 152$ cal BP, but in trench B it has an age of $37,213 \pm 681$ cal BP. In the test pit, the OES samples produced a range of 15,393 $\pm$ 120 cal BP to > 46 ka for occurrence E. Occurrence F is only represented by two samples (trench A: $26,048 \pm 142$ cal BP; trench B: $31,824 \pm 385$ cal BP). Ostrich eggshell dates for trench B, however, must be interpreted cautiously. Evidence for post-depositional mixing in trench B, first suggested by Gramly (1975, 1976), is supported by three Holocene dates (younger than ~10 ka) acquired from occurrences E and F by Tryon et al. (2015). Additionally, the new OES dates

indicate that Gramly's (1975, 1976) 5 to 10 cm arbitrary excavation levels may have crosscut sloping LSA and MSA strata leading to a mechanical mixture of artifacts from different natural and/or cultural levels. This could explain the ~7,000–10,000 year offset between trench A and the test pit in layers at the same depth below the surface in occurrence E (Tryon et al., 2015). Material found below 205 cm has been attributed to occurrence G by Tryon et al. (2015) and is constrained by the maximum date of > 46 ka in the test pit and the $26,048 \pm 142$ cal BP date on occurrence F from trench A. Since Gramly (1975, 1976) attributed material below occurrence E in the test pit to occurrence F, Tryon et al. (2015) conservatively group occurrences F and G into a ~26 to > 46 ka temporal unit.

The other three Lukenya Hill sites have been dated only by conventional radiocarbon methods on bone apatite. These dates are suspect and should be considered minimums due to the possibility of contamination with modern carbon from soil carbonates and humic acids (Brooks and Robertshaw, 1990; Kusimba, 2001; Higham et al., 2006). Marean (1990, 1992) identified two peaks in faunal and lithic density in the GvJm-62 assemblage, classifying one as terminal Pleistocene LSA and the other as Pleistocene LSA. The first peak, Marean's terminal Pleistocene LSA, is found at 70–180 cmbs and is associated with two dates: $11,950 \pm 460$ years BP (130–140 cmbs) and $12,195 \pm 330$ years BP (130–140 cmbs). The second peak, Marean's Pleistocene LSA, includes all material below 180 cm and is associated with a single date of $21,535 \pm 980$ years BP (220–230 cmbs; Merrick and Brown, 1984; Nelson and Kimengich, 1984; Marean, 1990; Marean and Gifford-Gonzalez, 1991; Barut, 1994, 1997). Kusimba (2001) acquired a fourth conventional radiocarbon date on bone apatite from the Bower-Nelson excavation of 8985 ± 270 years BP (50–60 cmbs). This date, however, is considered by Kusimba to be too young as it may be derived from an intrusive rodent burrow. While the conventional radiocarbon dates

probably underestimate the true ages of the GvJm-62 assemblage, it is not possible to be confident that all the material grouped by Marean (1990, 1992) into the 70–180 cmbs unit dates to the Pleistocene. In the GvJm-19 assemblage Marean (1990) identified an increase in dentition relative to bone, a shift in the lithic assemblage, and a change from sub-fossil to fully fossilized status at 110 cmbs. The material below 110 cm coincides with a conventional radiocarbon date of $13,705 \pm 430$ years BP (115–120 cmbs), confidently placing this part of the assemblage in the terminal Pleistocene. Six dates, ranging from 4145 ± 240 years BP to 8170 ± 1500 years BP, are reported for levels between 25 cmbs and 95 cmbs which date the ceramic and aceramic Holocene levels (Nelson and Kimengich, 1984; Marean, 1990; Kusimba, 2001). GvJm-46 was excavated in a series of test pits (1, 1B, 1C, 1D, 1E, 1F, 1G, 2, 3, 4, and 7). Only pits 3, 4, and 7 were placed to bypass a rock fall which restricted the depth of the other pits to between 160 cmbs and 200 cmbs (Miller, 1979). Two conventional radiocarbon dates of $19,330 \pm 945$ years BP (51–54 cmbs) and $20,780 \pm 1050$ years BP (87–90 cmbs) are reported for GvJm-46 (Nelson and Kimengich, 1984; Marean, 1990). No dates are reported for levels below 170 cm in test pits 3, 4, or 7, which Marean (1990) calls the MSA. Based on the stone tools recovered from depths below 170 cm, both Marean (1990, 1992) and Kusimba (2001) consider the MSA at GvJm-46 to be the oldest of the Pleistocene aged Lukenya Hill assemblages.

Archaeology Both Marean (1990, 1992) and Barut-Kusimba (1994, 1997, 2001) have provided comprehensive descriptions and discussions of the stone tool archaeology of the four Lukenya Hill sites included in this study. GvJm-22 was also restudied by Tryon et al. (2015). Gramly's (1975, 1976) excavations at GvJm-22 recovered > 50,000 stone artifacts and > 3000 faunal remains in a 21.75 m^2 area. A change in stone tool production is apparent between the occurrences with a shift from Levallois flake production and rare backed pieces in occurrence F

to an increased frequency of platform cores for blade and bladelet production in occurrence E. Scrapers are more common in occurrence F while backed pieces and retouched tools dominate occurrence E (Marean 1990, 1991; Barut, 1994, 1997; Kusimba, 2001; Tryon et al., 2015). All three studies agree that the assemblage ascribed to occurrence E, despite the different dates for the different trenches and the test pit found by Tryon et al. (2015), can be attributed to the LSA. Occurrences F and G (studied only by Tryon et al. 2015) are more difficult to interpret in the light of the new OES dates and the recognition of stratigraphic mixing. Tryon et al. (2015) stress that the material referred to occurrences F and G span the MSA-LSA transition, but due to the known post-depositional mixing may not necessarily represent a true transitional industry.

The Bower-Nelson assemblage from GvJm-62 was studied by Marean (1990, 1992). In that analysis, the Holocene LSA was found to be characterized by backed microliths and bladelets, while the Pleistocene LSA was determined to be dominated by large backed pieces. Microliths were rarely found in the Pleistocene LSA assemblage from the Bower-Nelson excavation (Marean, 1990). Kusimba's (2001) analysis of the lithic material recovered during the 1994 excavations at GvJm-62 focused on Level C (180–320 cmbs), which is roughly equivalent to Marean's (1990) Pleistocene LSA. Again, microliths were found to be rare, making up 12% of an assemblage dominated by scrapers and notched blades (Kusimba, 2001).

The LSA assemblage from GvJm-19 is the youngest and stylistically most standardized LSA assemblage from Lukenya Hill with crescents, curved backed blades, and curved microliths (Kusimba, 2001). The Holocene assemblages are distinct from the Pleistocene LSA assemblage, with the uppermost unit containing ceramics (Marean, 1990). GvJm-46 is the only Lukenya Hill site that can confidently be said to have distinct LSA and MSA units. In addition to backed microliths, the LSA unit contains outils ecailles, hammerstones, and what Miller (1979) calls a

fan scraper. Both Marean (1990) and Kusimba (2001) describe Miller's fan scraper as resembling the convex thumbnail scrapers found in the Enkapune Ya Muto Sakutiek Industry (Ambrose, 1998b). If this comparison is accurate, it is likely that the bone apatite radiocarbon dates are underestimates by 10,000–15,000 years. Unfortunately, only a very small faunal assemblage, not large enough to warrant sampling, was recovered from the LSA layers above 170 cm in the test pits. The MSA is separated from the LSA by a rock fall and two sterile strata. As such, it is unlikely that a transitional industry is represented at GvJm-46. The MSA at GvJm-46 contains no backed microliths or Miller's fan scrapers. Instead, the assemblage is dominated by large blades and denticulate scrapers (Marean, 1990; Kusimba, 2001).

The faunal assemblages of the Lukenya Hill sites are dominated by arid-adapted taxa not found in the region today, including the extinct alcelaphine *Damaliscus hypsodon*, Grevy's zebra (*Equus grevyi*), and oryx (*Oryx beisa*; Marean 1990, 1992; Marean and Gifford-Gonzalez, 1991; Barut, 1994; Faith et al., 2012). Conspicuously rare in the archaeological assemblages are warthog (*Phacochoerus* sp.), waterbuck (*Kobus ellipsiprymnus*) and impala (*Aepyceros melampus*), which are common in the moist grasses that have historically characterized the open savannas around Lukenya Hill. Marean (1990, 1992) attributes this lack of modern fauna in the archaeological record to more arid conditions and drier grasslands during the Late Pleistocene than at present. Differences in species representation or diversity between the Lukenya Hill sites are attributed to whether the site is a rockshelter/overhang (GvJm-22 and GvJm-19) or open-air (GvJm-62 and GvJm-46), which may be related to site function as proposed by Marean (1990, 1997) and/or reflect different post-depositional processes as indicated in the study of GvJm-22 by Tryon et al. (2015). When grouped by time as opposed to site, Marean (1990, 1992) finds that the Late Pleistocene is dominated by dry grass grazers and hartebeest (*Alcelaphus buselaphus*), a

moist grass grazer that can also survive on dry grasses. Mixed feeding and browsing taxa are rare in the Pleistocene Lukenya Hill assemblages. Overall, there are little or no taxonomic differences between MSA and LSA strata, or LSA strata of different ages, at Lukenya Hill. Micromammals studied by Tryon et al. (2015) support Marean's (1990, 1992) reconstruction of a semi-arid savanna environment likely drier than at present.

Kalemba Rockshelter

Kalemba Rockshelter is situated approximately 1200 m above sea level in a mass of Archaean granite located in a steep and narrow valley in the eastern Zambian Highveld near the present-day town of Chadiza in Zambia's Eastern Province (Figure 1). Today, the surrounding hill country is characterized by extensive grasslands with wooded biomes restricted to riverine areas. The site is located in an intermediate zone between wet and dry Zambezian Miombo woodlands, but the Highveld, between 1100 and 1400 m above sea-level, is characterized more precisely as *Colophospermum* mopane woodland (Phillipson, 1973, 1976, 1977; White, 1983). Climate in this region is mild with mean annual temperatures between 17 and 20°C and mean annual rainfall around 600 mm (Vincent et al., 1961; White, 1983). Kalemba, which is the largest known rockshelter in Zambia, was excavated by David Phillipson in 1971. Phillipson (1973, 1976) excavated the site in 47 layers which were then grouped into 13 stratigraphic horizons representing a cumulative thickness of 4.3 m. The horizons were labeled from G at the base of the sequence to S at the surface. Phillipson (1976) further grouped these horizons into four Pleistocene occupations: MSA, MSA/LSA transition, the 'Nachikufan I' (LSA), and the Makwe Industry (late LSA). While Phillipson's Makwe Industry, or late LSA, occupation may date to the earliest Holocene, it is included here as interpreted by Phillipson (1973, 1976) in having

continued occupation by the 'Nachikufan I' inhabitants. The top of the Kalembe sequence contains early and later Iron Age occupations that are not included in this study.

Chronology The Kalembe Rockshelter sequence has been dated by conventional radiocarbon analysis, primarily on bone apatite. As at Lukenya Hill, recrystallization of bone with inclusions of modern carbon (Higham et al., 2006) most likely results in dates which underestimate the true ages of the deposits. A minimum date of > 37 ka from the base of the excavation dates the sole MSA horizon, G, in excavation levels 47 and 46. The MSA-LSA transitional industry is found in Horizons H, I, and J, and the bottom of Horizon K between excavation levels 45 and 30. Two dates of $24,600 \pm 2000$ years BP (Horizon H; level 40) and $24,420 \pm 2000$ years BP (bottom of Horizon K; level 30) suggested to Phillipson (1973, 1976) a significant hiatus in occupation between the MSA and MSA-LSA transition. Phillipson (1976) split Horizon K between the MSA-LSA transition occupation and the LSA 'Nachikufan I' occupation (top of Horizon K through Horizon N; levels 29 to 15) due to the presence of a rock fall within the horizon just above excavation level 30. Combined with the appearance of the 'Nachikufan I' lithic industry and a conventional radiocarbon date of $14,800 \pm 1000$ years BP from the top of Horizon K (level 27), Phillipson believed the rock fall represented a second occupational hiatus (Phillipson, 1973, 1976). The same split of Horizon K is applied here, with samples from below the rock fall considered to be from the MSA-LSA transition and those above the rock fall to be from the LSA. Dates for Horizons L (> 31 ka; level 24) and M ($26,300 \pm 1500$ years BP; level 19), however, are older than the two ages for the MSA-LSA transition. Additionally, the date for Horizon N ($15,330 \pm 1100$ years BP; level 15) is older than the one for the top of Horizon K (Phillipson, 1976). These significantly inverted dates call into question the evidence for an extended occupational hiatus between the MSA-LSA transition and the LSA. The late LSA, or Makwe

460 Industry, occupation is represented by Horizons O and P between excavation levels 14 and 10. A
 461 conventional radiocarbon date on bone apatite from the middle of Horizon O provides a date of
 462 7915 ± 300 years BP (level 12). Phillipson (1973, 1976) also acquired two conventional
 463 radiocarbon dates on charcoal from the late LSA: 6810 ± 105 years BP (top of Horizon O; level
 464 11) and 7030 ± 105 years BP (Horizon P; level 10). The Iron Age occupations (Horizons Q, R,
 465 and S) are dated by conventional radiocarbon dates on charcoal (Horizon Q) and beans from a
 466 pot (Horizon S). The early Iron Age, Horizon Q (5040 ± 110 years BP and 4480 ± 90 years BP),
 467 dates to the mid-Holocene, while the later Iron Age, Horizon S (115 ± 70 years BP), is virtually
 468 modern (Phillipson, 1973, 1976). The entire pre-Iron Age assemblage is included in this study.
 469 Archaeology Phillipson (1976) describes the Kalembe lithic assemblage as grading from Mode 3
 470 ‘Stillbay-like’ during the MSA occupation to the ‘Nachikufan I’ and Makwe Industry by the
 471 LSA and late LSA occupations, respectively. Kalembe’s MSA and MSA-LSA transition units
 472 are dominated by scrapers and unifacial points. Backed tools first appear during the transitional
 473 horizons. The appearance of geometrics signifies the beginning of the ‘Nachikufan I’ LSA
 474 (Phillipson, 1973, 1976). The late LSA Makwe Industry is predominantly composed of
 475 microliths. Phillipson (1973, 1976) stresses that there are no breaks in the developmental history
 476 of the lithic assemblage at Kalembe, even if there are one or more occupational hiatuses. Most
 477 of the fauna at Kalembe (~75%) can be characterized as grazers, with the assemblage being
 478 dominated by Burchell’s zebra (*Equus quagga*). Mixed feeders, like oribi (*Ourebia ourebi*), and
 479 browsers, including the common bush duiker (*Sylvicapra grimmia*), are present in the MSA and
 480 MSA-LSA transition assemblages. These periods are interpreted to have had greater woody
 481 cover, perhaps around streams or seasonal water holes, than in the LSA and the late LSA. By the
 482 LSA, the faunal assemblage is almost exclusively grazers and is dominated by zebra. Mixed

feeding taxa become common again at the end of the LSA and into the late LSA. These shifts in faunal community structure led Phillipson (1973, 1976) to suggest that the LSA was characterized by drier and cooler conditions than in either the MSA-LSA transition or today. Phillipson's (1973, 1976) interpretation of the late LSA faunal community included a change in climate from the LSA to more humid and wooded conditions, although not to the extent of the MSA or MSA-LSA transition occupations, the development and use of new hunting techniques paralleling the development of the 'Nachikufan I' to the Makwe Industry (e.g. Phillipson, 1980), or some combination of both.

Chronological Control and Correlating Climatic Patterns

A series of factors – high-latitude glacial cycles, Walker circulation intensification, El Nino and Indian Ocean Dipole variability, orbital forcing, and high-latitude millennium-scale events – drove increased environmental pressure on African ecosystems and mediated local paleoenvironments during the Late Pleistocene (Zachos et al., 2001; deMenocal, 2004; Kingston, 2007; Trauth et al., 2009). The significant uncertainties in the chronologies of each of the study sites, however, make it difficult, if not impossible, to correlate the environmental and climatological reconstructions based on the stable isotope data presented below with specific environmental records, such as lake cores or pollen records, or climatological events, such as the Last Glacial Maximum or the Heinrich 1 Event. In the interest of avoiding a false sense of accuracy in fitting data presented here with particular records or events, the results below will be presented, interpreted, and discussed on a site by site basis without any further explicit discussion of chronology. While this is a less than ideal approach, it does offer an honest presentation of stable isotope data, which provides the site-specific environmental information

that has been lacking from recent climate modeling studies and syntheses addressing the MSA-LSA transition (e.g., Barham, 2000; Basell, 2008; Chase, 2010; Blome et al., 2012; Scerri, 2013; Tryon and Faith, 2013, 2016; Tryon et al., 2014; Trauth et al., 2015). Only when more reliable dates for many of these sites are published can we then correlate site-specific environmental records with well-dated regional and global environmental records and climatic events.

Materials and methods

Stable isotope analysis of fossil tooth enamel

Stable isotope characterization of fossil faunal tooth remains for paleoecological reconstructions is a well-known archaeological research approach (Lee-Thorp, 1989; Kohn, 1996, 2010; Sponheimer and Lee-Thorp, 1999a, b; Cerling et al., 2003, 2015; Schoeninger et al., 2003; Kingston and Harrison, 2007; Harris et al., 2008). The carbonate fraction of tooth enamel is minimally affected by diagenesis and can be used as a proxy for diet and drinking behavior (DeNiro and Epstein, 1978; Wang and Cerling, 1994; Cerling and Harris, 1999; Sponheimer and Lee-Thorp, 1999a; Lee-Thorp, 2002; Lee-Thorp and Sponheimer, 2003). This study infers ecological, environmental, and climatic contexts based on the signatures of these feeding and drinking habits. The use of a community-based approach is an effort to mitigate the effects of seasonality, migration, and taxon-specific physiology on the link between diet and environment (Caswell et al., 1973; Behrensmeyer and Hook, 1992). Carbon and oxygen isotopic composition is reported in δ -notation where $\delta^{13}\text{C}$ or $\delta^{18}\text{O} = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{18}\text{O}/{}^{16}\text{O}$, and δ is expressed in per mil, ‰, i.e., $\times 1000\text{‰}$. Carbon and oxygen values are reported relative to VPDB (Vienna Pee Dee Belemnite).

Stable carbon isotopic signatures of both modern and fossil herbivore tooth enamel are

529 related to the isotopic composition of vegetation in the food chain (Tiezen et al., 1983; Ambrose
 530 and DeNiro, 1986; Cerling and Harris, 1999; Cerling et al., 2003, 2015). Trees, shrubs, and high-
 531 altitude grasses (> 2,000 m) utilize the C₃ photosynthetic pathway and have a modern $\delta^{13}\text{C}$ range
 532 of -22‰ to -36‰ (mean: $-27.4 \pm 2.0\text{‰}$). Under water-stressed conditions C₃ biomass is ¹³C-
 533 enriched with a mean $\delta^{13}\text{C}$ value of $-24.6 \pm 1.1\text{‰}$ (Tiezen et al., 1979, 1983; O’Leary, 1981,
 534 1988; Ambrose and DeNiro, 1986; Cerling et al., 2003, 2015; Passey et al., 2005; Sponheimer et
 535 al., 2003; Kohn, 2010). Variability in C₃ plants is partially driven by photosynthetic recycling of
 536 respired CO₂ in closed canopy forests, or the canopy effect, and variability in water availability,
 537 light, and temperature (van der Merwe and Medina, 1991; Kohn, 2010). There is an increase in
 538 ¹³C in C₃ plants from wet to mesic and xeric habitats with $\delta^{13}\text{C}$ being most enriched in open, arid
 539 environments (Heaton, 1999; Kingston and Harrison, 2007). C₄ subpathways characterize most
 540 of the low elevation grasses in tropical Africa and have $\delta^{13}\text{C}$ values ranging from about -14‰ to
 541 -10‰ (mean: $-12.7 \pm 1.2\text{‰}$; Heaton, 1999; Harris and Cerling, 2002; Passey and Cerling, 2002;
 542 Cerling et al., 2003). Arid adapted C₄ grasses use the NAD-me and PEP-ck subpathways
 543 (Hattersley, 1992; Chapman, 1996) and have an average $\delta^{13}\text{C}$ value of $-13.0 \pm 0.7\text{‰}$ (Cerling et
 544 al., 2003, 2015). C₄ grasses in more mesic environments utilize the NADP pathway with an
 545 average $\delta^{13}\text{C}$ of $-11.8 \pm 0.2\text{‰}$ (Cerling et al., 2003, 2015). Succulents fix CO₂ through the CAM
 546 (Crassulacian acid metabolism) pathway and yield isotopic values between C₃ and C₄ plants
 547 (O’Leary, 1981, 1988; Heaton, 1999), but it is unlikely that succulents comprised a significant
 548 component of Central and East African herbivore diets during the Late Pleistocene and they are
 549 not considered further in this study (Cerling et al., 2003; Kingston, 2011; Garrett et al., 2015).
 550 The non-overlapping nature of $\delta^{13}\text{C}$ ranges for most modern African C₃ and C₄ plants are ideal
 551 for differentiating between browsers, grazers, and intermediate, or mixed, feeders based on gross

feeding strategy.

To compensate for recent changes in atmospheric CO₂, all $\delta^{13}\text{C}$ values of fossil enamel in this study are adjusted by -1.5‰ following established conversion methods (Tippie et al., 2010; Faith et al., 2015; Garrett et al., 2015). In addition to atmospheric CO₂, the fractionation between diet and enamel tissue must be considered. Tooth enamel of large mammals has been shown to be ~+14.1‰ enriched in ^{13}C compared to their diet (Cerling and Harris, 1999; Passey et al., 2005). As such, enamel values more depleted than -9‰ characterize C₃ dominated diets, values more enriched than -3‰ suggest primarily C₄ diets, and values in-between indicate mixed feeding.

Analysis of the oxygen isotope composition ($\delta^{18}\text{O}$) of tooth enamel provides a proxy for water flux and oxygen exchange in body water – a function of drinking water, the water from ingested foods, the $\delta^{18}\text{O}$ of metabolic and atmospheric oxygen, and animal behavioral and physiological water conservation mechanisms (Longinelli, 1984; Koch et al., 1989; Kohn, 1996; Koch, 1998; Sponheimer and Lee-Thorp, 1999b). It is used here as an indicator of aridity with the assumption that during arid intervals in tropical low latitudes the lighter oxygen isotope, ^{16}O , will be preferentially lost in evaporative processes relative to the heavier, ^{18}O , isotope. The result of this scenario is heavier, or ^{18}O enriched, signals recorded in faunal tooth enamel (Kohn, 1996; Levin et al., 2006). C₃ plant leaves have enriched values compared to surface water sources due to the evapotranspiration of leaf water. As such, browsing taxa which rely on leaf water typically have higher $\delta^{18}\text{O}$ values than grazing taxa which drink primarily from surface sources. This difference is most evident in the dry season when evapotranspiration of leaf water is at its highest. Mixed feeders tend to have greater seasonal variation in their $\delta^{18}\text{O}$ values than browsers and grazers. During the rainy season they consume fresh green grass and have lower $\delta^{18}\text{O}$ values,

but in the dry season they include more C₃ browse and water derived from plant leaves in their diets, leading to higher $\delta^{18}\text{O}$ values. Therefore, higher $\delta^{18}\text{O}$ is associated with lower $\delta^{13}\text{C}$ in herbivores, especially mixed feeders (Ambrose, 1991; Sponheimer and Lee-Thorp, 1999a, b, 2001, 2003, 2007; Cerling et al., 2008). Species that acquire most of their water from leaves track evaporative water deficit. The difference between taxa that obtain water from leaves and those that obtain water from surface sources can be used to calculate an aridity index (Levin et al., 2006). Such an aridity index, however, is not calculated here due lacking adequate sample sizes for the necessary taxa.

Materials, sampling, and laboratory techniques

Stable carbon and oxygen isotopes were generated on 237 total samples of powdered fossil herbivore tooth enamel of known provenience sampled from the archaeological collections at the National Museum of Ethiopia (Porc Epic), the National Museums of Kenya (Lukenya Hill), and the Livingstone Museum, Zambia (Kalemba Rockshelter) between May and July of 2013 (Table 1). All catalog numbers and provenience information is provided in the Supplementary Online Material (SOM) Table S1. In an attempt to minimize sampling multiple teeth from the same individual, only a single tooth was sampled from partial or complete tooth rows. Sampling focused on herbivore communities, including Bovidae, Equidae, and Suidae. Special care was taken to ensure that similar communities were sampled through time at each site to increase the reliability of comparisons and identified patterns through time.

Powdered enamel samples were collected from molars, preferably third molars, identifiable to a specific taxon. The sampling of later-forming teeth limits the potentially confounding effects of weaning and juvenile dietary signals. Each tooth was carefully cleaned of

adhering sediment and weathering rinds using a high-speed Brasseler dental drill (Forza L50k) with tapered carbide burs. Approximately 2 mg of powdered enamel was collected from each tooth by drilling a vertical line from the cement-enamel junction to the occlusal surface along broken edges. This process is minimally destructive, preserves the crown of the tooth, and ensures homogenization of intra-tooth variability for bulk isotopic averages (Kingston and Harrison, 2007; Sponheimer and Lee-Thorp, 2007). Samples were reacted with commercially available bleach (NaOCl) diluted 50% for 24 hours in 1.5 mL microcentrifuge tubes to digest organic contaminants. Samples were then rinsed and centrifuged to a neutral pH with double distilled water. This was followed by sample treatment with 0.1 M acetic acid for 4 hours to remove secondary carbonates. Samples were again rinsed to neutrality with double distilled water and then freeze-dried. Enamel samples were reacted with 100% phosphoric acid at 70°C in a Kiel III carbonate extraction device interfaced with a Finnigan-MAT 252 isotope ratio mass spectrometer at the Light Stable Isotope Laboratory, Department of Geosciences, University of Florida, Gainesville. Analytical precision was measured by repeated analysis of the international calcium carbonate standard NBS-19. Means and standard deviations of 103 replicates of NBS-19 for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are $2.08 \pm 0.04\text{‰}$ and $-1.99 \pm 0.07\text{‰}$, respectively.

Statistics

Statistical analyses were performed using SPSS ver. 23 (2015). While care was taken to ensure that all teeth could be identified to a specific taxon, for some statistical analyses herbivore taxa were divided into trophic categories based on observational (Kingdon, 1982, 2015) and isotopic (Harris and Cerling, 2002; Sponheimer et al. 2003; Cerling et al., 2003, 2015) data: browsers (*Madoqua*, *Neotragus*, *Raphicerus*, *Sylvicapra*, *Tragelaphus oryx*, and *Tragelaphus*

scriptus), mixed feeders (*Aepyceros*, *Eudorcas*, *Nanger*, *Ourebia*, *S. antiquus*, *Tragelaphus strepsiceros*), fresh grass grazers (*S. caffer*, *Kobus*, *Redunca*), grazers (*Alcelaphus*, *Connochaetes*, *Damaliscus*, *Hippotragus*, *Oryx*, *Equus*, and *Phacochoerus*), and omnivores (*Potamochoerus*). When potential temporal bins and/or trends were inferred from the descriptive statistics at a study site, both individual species and the trophic categories described above were analyzed with Mann-Whitney U and Kruskal-Wallis non-parametric statistical tests in order to characterize how $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ changed at the site. Identifying meaningful temporal changes in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel values requires that there be coherency within the trophic categories despite uneven sampling of individual species. To demonstrate coherency within these categories, 95% confidence intervals (CI) for the mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel values of each taxon at each site where temporal trends were suggested was calculated by bootstrapping with replacement over 10,000 iterations. Results of non-parametric tests are considered significant at the $p < 0.05$ level. It must be noted that statistical analysis alone does not provide an indication of real climatological or phytogeographical change, but rather an indication of a difference between isotopic values for different time periods which can be further interpreted. In addition to descriptive and non-parametric statistics, the relative contribution of C_3 and C_4 biomass to diet is estimated from the $\delta^{13}\text{C}$ enamel values using a mixing model between end-member $\delta^{13}\text{C}$ values for C_3 and C_4 plants and the +14.1‰ enrichment factor between diet and tooth enamel (Phillips, 2012; Cerling et al., 2015; Garrett et al., 2015):

$$\delta^{13}\text{C}_{\text{measured}} = \delta^{13}\text{C}_{\text{C}_3} * f_{\text{C}_3} + \delta^{13}\text{C}_{\text{C}_4} * f_{\text{C}_4},$$

where $\delta^{13}\text{C}_{\text{C}_3}$ and $\delta^{13}\text{C}_{\text{C}_4}$ are the assumed end-member values. While a variety of end-member estimates can be derived by considering temperature, humidity, water stress, CO_2 concentration, and vegetative functional type (Kohn, 2010; Diefendorf et al., 2010; Katoh et al., 2016), the three

sets of end-member assumptions calculated in this study are intended to be directly comparable to those of Garrett et al. (2015), who provided one of the few thorough stable isotope studies addressing the MSA in East Africa. The first set of end-member assumptions uses the mean values for C₃ and C₄ biomass derived from extensive analyses of modern plants discussed above (-27.4 ± 2.0‰ and -12.7 ± 1.2‰, respectively; Cerling et al., 2003; Passey et al., 2005; Kohn, 2010). The second uses the mean value for C₃ biomass under water-stressed conditions (-24.6 ± 1.1‰; Cerling and Harris, 1999; Passey et al., 2005) and an unaltered value for C₄ biomass. The third calculation uses the water-stressed value for C₃ biomass again, but also uses an arid end-member for C₄ biomass (-13.0 ± 0.7‰) based on the combined mean of NAD-me and PEP-ck grasses (Hattersley, 1992; Chapman, 1996). The first two sets of end-member assumptions are ones used by Garrett et al. (2015). The third set of assumptions, considering water-stressed, or arid, end-members, for both C₃ and C₄ biomass, is calculated here since the environments at all of the study sites have previously been interpreted as cooler and drier than at present. An unlimited number of end-member assumptions could hypothetically be derived for this mixing model, but the resulting percentages of C₃ and C₄ biomass consumption are only intended to be estimates and are most useful if they can be directly compared to other temporally relevant datasets. End-member values do not need to be corrected for changes in atmospheric CO₂ since all fossil data have been adjusted to modern values.

Hypotheses

Fossil ungulate enamel isotope data from each study site are interpreted with reference to site-specific expectations.

Porc Epic The shift from a faunal assemblage dominated by fresh grass feeding reduncines

earlier in the sequence to dry grass feeding alcelaphines (Assefa 2002, 2006) later suggests that $\delta^{13}\text{C}$ enamel values will become lower, or shifted further in a C_3 direction, over time. These lower $\delta^{13}\text{C}$ values should correspond with higher $\delta^{18}\text{O}$ values.

Lukenya Hill As discussed above, no significant taxonomic differences were found between MSA and LSA strata either within individual sites or across all four of the Lukenya Hill sites (Marean, 1990, 1992; Marean and Gifford-Gonzalez, 1991). The lack of significant remains of warthog, waterbuck, and impala in all four of the Lukenya Hill archaeological assemblages, but the presence of historically absent or extinct taxa, like oryx and *D. hypsodon*, implies dry and open conditions during both the MSA and LSA at Lukenya Hill (Marean and Gifford-Gonzalez, 1991; Marean, 1992). Based on the analysis of the faunal assemblages collected from the four Lukenya Hill sites, no change in $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ values are expected between MSA and LSA units, or LSA units of different ages.

Kalemba Rockshelter The increasing dominance of grazers, particularly *Equus*, at Kalemba leads to an expectation of higher $\delta^{13}\text{C}$ enamel values over time, especially from the MSA through LSA occupations. Phillipson's (1973, 1976) interpretation of progressively more open and arid environments from the MSA to the LSA suggests higher $\delta^{18}\text{O}$ over time as well. The late LSA was described as more humid and wooded than the LSA (Phillipson, 1976). As such, a shift to lower $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values is expected between these occupations at Kalemba.

Results and preliminary discussion

Porc Epic

Between 52% (normal-condition end-members) and 43% (water-stressed C_3 end-member) of individuals at Porc Epic were estimated to have consumed > 70% C_4 biomass. Plains

zebra, which yielded low $\delta^{13}\text{C}$ and high $\delta^{18}\text{O}$ values ($n = 4$; $\delta^{13}\text{C}$: $-2.5 \pm 1.3\text{‰}$; $\delta^{18}\text{O}$: $2.5 \pm 1.8\text{‰}$), is typical of most taxa at Porc Epic (Table 2). This pattern of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values suggest less green grass feeding and more dry grass and C_3 feeding which tends to indicate high aridity. The interpretation of high aridity and dry grass feeding is supported by estimates of C_4 biomass consumption by African buffalo (*S. caffer*), which range from 86% – 82% depending on mixing model. Modern African buffalo averages ~95% – 90% C_4 consumption (Cerling et al., 2015). Open conditions are further indicated by kudu (*T. strepsiceros*), a mixed feeder, which averages less than 25% C_4 consumption today (Cerling et al., 2015), but ranged between 27% (C_3 and C_4 arid end-members) and 42% (normal-conditions end-member) at Porc Epic. Under the mixing model assuming arid end-members for both C_3 and C_4 biomass, 45% of individuals at Porc Epic was estimated to have consumed > 70% C_4 biomass. Low variability in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for zebra, impala, and tsessebe (*Damaliscus lunatus*) may indicate little or no change through time. Other taxa, however, had much greater variability in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. For example, warthog ($n = 13$) has $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ means and standard deviations of $-3.6 \pm 3.0\text{‰}$ and $1.5 \pm 2.1\text{‰}$, respectively (Table 2).

The higher variability in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for some taxa at Porc Epic led to an investigation of possible changes through time using the 160 cmbs level as a break point. It is at 160 cmbs that differences in faunal community composition and ochre use and manufacture (Assefa, 2006; Rosso et al., 2014) have previously been identified. Low sample sizes ($n \leq 3$) for one or both of the two time bins precludes statistical analyses on individual species, but sample sizes are increased to an appropriate level when taxa are grouped into trophic categories. The extinct taxon *S. antiquus* was grouped with the mixed feeders at Porc Epic based on the combination of low $\delta^{13}\text{C}$ ($-6.5 \pm 1.2\text{‰}$) and high $\delta^{18}\text{O}$ ($3.5 \pm 3.3\text{‰}$) values, which is suggestive

of mixed feeding behavior (Table 2). It is unclear what the feeding habit of *S. antiquus* at Porc Epic may have been since its exceptionally long horns would seem to make feeding on C₃ resources a challenge. It is possible that this is an artifact of Assefa's (2002) identifications, but it is interesting to note that the teeth assigned to *S. antiquus* and *S. caffer* ($\delta^{13}\text{C}$: $-0.7 \pm 3.0\text{‰}$) by Assefa were separated isotopically. When trophic categories were split into analytical units above and below 160 cmbs, the only possible temporal trend revealed was indicated by non-overlapping CIs of $\delta^{18}\text{O}$ for mixed feeders (Table 3). This result, however, was not supported by a Mann-Whitney U test ($p = 0.076$), perhaps due to the small sample size of mixed feeders ($n = 2$) for the below 160 cmbs unit. Without statistical support it must be assumed that there is no significant change over time in the $\delta^{18}\text{O}$ values of mixed feeders (Figure 2A). Mixed feeders have overlapping CIs for $\delta^{13}\text{C}$ (Figure 2B). No other trophic categories were found to have non-overlapping CIs for $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ values, and additional Mann-Whitney U tests failed to find any significant differences between the time bins (Table 3; Figure 2A, B).

Lukenya Hill

GvJm-22 The small sample size from the test pit ($n = 4$), and the fact that three separate taxa were sampled, preclude meaningful results or interpretations from the test pit. Additionally, the small sample ($n = 2$) from the post-depositionally mixed trench B assemblage will not be discussed. Trench A is represented by five samples, three of which are *D. hypsodon*. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ means for *D. hypsodon* from trench A were $0.0 \pm 1.9\text{‰}$ and -0.6 ± 0.7 , respectively. The small sample size prevents any investigation of temporal changes. A total of 35 samples were collected from trench C and the C+ balk assemblages (Table 4). Regardless of mixing model, 80% of individuals represented by these samples were estimated to have consumed >

70% C₄ biomass. All grazing and mixed feeding taxa in trench C and C+ balk at GvJm-22 had high $\delta^{13}\text{C}$ values and low $\delta^{18}\text{O}$ with low variability (Table 4). These results suggest that there are no, or very small, changes in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values over time.

GvJm-22 has been split based on the lithic assemblage into occurrence E, with an LSA lithic industry, and occurrence F, which contains MSA in addition to LSA tools. Due to this pre-existing division, a comparison of these two units was undertaken despite the rather small variability in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for all taxa at GvJm-22. *Damaliscus hypsodon* ($n = 14$), with high $\delta^{13}\text{C}$ ($-0.2 \pm 1.0\text{‰}$) and low $\delta^{18}\text{O}$ ($-1.9 \pm 1.5\text{‰}$) was categorized as a surface-water drinking grazer (Table 4). All individuals of *D. hypsodon* were estimated to have consumed > 70% C₄ biomass regardless of mixing-model condition. Grazers are the only trophic category analyzed since they account for 30 of the 35 samples from GvJm-22. No temporal changes were found in $\delta^{13}\text{C}$ ($p = 0.705$) or $\delta^{18}\text{O}$ ($p = 0.184$) through a Kruskal-Wallis analysis with three bins: occurrence E, occurrence F, and the 150–170 cmbs material found between occurrences E and F. The results did not change if the two samples from between occurrences E and F were removed from the analysis (Mann-Whitney U tests - $\delta^{13}\text{C}$: $p = 0.963$; $\delta^{18}\text{O}$: $p = 0.091$). This may not be particularly surprising since all three bins have largely overlapping CIs for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. The most common taxon, *D. hypsodon*, however, did appear to have different $\delta^{18}\text{O}$ values between occurrences E ($n = 9$; $-1.2 \pm 1.1\text{‰}$; CI: -1.8‰ to -0.5‰) and F ($n = 4$; $-3.8 \pm 0.5\text{‰}$; CI: -4.3‰ to -3.3‰). The two occurrences had non-overlapping CIs for $\delta^{18}\text{O}$, with occurrence E having higher $\delta^{18}\text{O}$ values than occurrence F. These values suggest that occurrence E represents a more arid interval than occurrence F. A Mann-Whitney U ($p = 0.003$) provided statistical support for the difference between occurrences E and F. No difference was identified between occurrences E and F in the $\delta^{13}\text{C}$ values of *D. hypsodon* (Mann-Whitney U: $p = 0.710$). Small

sample sizes prevent comparisons between occurrences E and F for other taxa.

GvJm-62 Fifteen samples were obtained from the Pleistocene LSA levels of GvJm-62. With the exception of one sample of Thomson's gazelle (*Eudorcas thomsonii*), all samples from GvJm-62 came from grazing taxa. Depending on end-members, 87% (normal-condition end-members), 80% (C_3 and C_4 arid end-members), or 73% (water-stressed C_3 end-member) of the samples were estimated to have consumed $> 70\%$ C_4 biomass. *Damaliscus hypsodon* ($n = 5$; $\delta^{13}C$: $0.6 \pm 0.4\text{‰}$; $\delta^{18}O$: $-3.9 \pm 1.0\text{‰}$), hartebeest ($n = 4$; $\delta^{13}C$: $0.1 \pm 1.5\text{‰}$; $\delta^{18}O$: $-4.7 \pm 1.0\text{‰}$), and zebra ($n = 4$; $\delta^{13}C$: $-2.6 \pm 1.2\text{‰}$; $\delta^{18}O$: $-2.7 \pm 0.8\text{‰}$) represented most of the samples from GvJm-62 (Table 4). All individuals of *D. hypsodon* were estimated to have consumed $> 70\%$ C_4 as at GvJm-22. The low variability in $\delta^{13}C$ and $\delta^{18}O$ values for all of these taxa may reflect a restricted stratigraphic distribution with most samples (13 of the 15) coming from between 220 cmbs and 270 cmbs.

GvJm-19 GvJm-19 has the lowest number of individuals estimated to have consumed $> 70\%$ C_4 biomass. All mixing models put the percent of high C_4 consuming individuals at $\leq 73\%$. While only 11 samples came from GvJm-19, the lower C_4 consumption was supported by the combination of low $\delta^{13}C$ values and high $\delta^{18}O$ values (Table 4). For example, hartebeest ($n = 3$), which has the lowest $\delta^{18}O$ of any species sampled at GvJm-19, had $\delta^{13}C$ and $\delta^{18}O$ means of $-1.6 \pm 0.8\text{‰}$ and $-2.8 \pm 1.1\text{‰}$, respectively. Hartebeest diet at GvJm-19 was estimated to have included between 69% and 85% C_4 biomass, well below the modern average of $\sim 95\% - 90\%$ (Cerling et al., 2015). This combination of $\delta^{13}C$ and $\delta^{18}O$ values is indicative of generally arid conditions and would correspond with increased dry grass and C_3 feeding. Only 55% of individuals sampled at GvJm-19 were estimated to have consumed $> 70\%$ C_4 biomass using the

mixing model which assumes arid end-members for both C₃ and C₄ biomass.

GvJm-46 The MSA faunal assemblage from GvJm-46 is almost entirely made up of *D. hypsodon*. Marean (1990, 1992) found that 92% (115 out of 125) of the identifiable dentition and postcrania can be attributed to *D. hypsodon*. It is thus not surprising that 15 of the 17 samples from GvJm-46 are of *D. hypsodon*. These samples yielded high $\delta^{13}\text{C}$ ($0.7 \pm 1.0\text{‰}$) and low $\delta^{18}\text{O}$ ($-3.7 \pm 1.1\text{‰}$) means, which implies humid conditions and abundant green grass available for consumption (Table 4). All individuals sampled from GvJm-46 were estimated to have consumed $\geq 87\%$ C₄ biomass.

Lukenya Hill Summary The significant difference in $\delta^{18}\text{O}$ values for *D. hypsodon* found between occurrences E and F at GvJm-22 leads one to wonder if there are trends across the four Lukenya Hill sites. With the uncertainties surrounding the chronologies of the Lukenya Hill sites, the most conservative way to search for trends in $\delta^{13}\text{C}$ and/or $\delta^{18}\text{O}$ values is to aggregate them by artifact typology. Two different sets of aggregates are considered here (Table 5). The first sorts the sites into MSA and LSA units with GvJm-46 and occurrence F at GvJm-22 in the MSA and occurrence E at GvJm-22, GvJm-62, and GvJm-19 in the LSA. The second uses three units by recognizing occurrence F at GvJm-22, which contains a mixed assemblage of MSA and LSA artifacts, as its own unit between the MSA and the LSA. This grouping is not intended, however, to suggest that occurrence F represents a true MSA-LSA transitional industry. In both sets of aggregates (MSA versus LSA Mann-Whitney U: $p = 0.014$; MSA versus F versus LSA Kruskal-Wallis: $p = 0.016$) significant differences were found between the units in the $\delta^{18}\text{O}$ values of *D. hypsodon* (Table 5). The trend over time, as inferred from the slightly overlapping CIs (MSA: -

4.2‰ to -3.1‰; F: -3.6‰ to -1.7‰; LSA: -2.7‰ to -1.2‰), was clearly towards higher $\delta^{18}\text{O}$ values. For neither aggregate (MSA versus LSA Mann-Whitney U: $p = 0.101$; MSA versus F versus LSA Kruskal-Wallis: $p = 0.086$) were significant differences found in the $\delta^{13}\text{C}$ values of *D. hypsodon* between the units. Considering the grazer trophic category, which accounts for 76 of the 89 total Lukenya Hill samples, significant differences (MSA versus LSA Mann-Whitney U: $p = 0.049$; MSA versus F versus LSA Kruskal-Wallis: $p = 0.046$) between the units were again found for $\delta^{18}\text{O}$ (Table 5; Figure 3A). As with *D. hypsodon*, the trend was towards higher $\delta^{18}\text{O}$ values over time (MSA CI: -4.0‰ to -2.8‰; F CI: -3.3‰ to -1.9‰; LSA CI: -2.7‰ to -1.7‰). No significant differences were found in $\delta^{13}\text{C}$ values between the units (MSA versus LSA Mann-Whitney U: $p = 0.136$; MSA versus F versus LSA Kruskal-Wallis: $p = 0.067$; Figure 3B). The shift towards higher $\delta^{18}\text{O}$ values from the MSA to the LSA is indicative of more arid conditions over time (Figure 3A).

Kalemba Rockshelter

Between 48% (water-stressed C_3 end-member) and 58% (normal-condition end-member) of individuals sampled from Kalemba were estimated to have consumed > 70% C_4 biomass. Zebra, the most common grazer ($n = 34$) at Kalemba, had low $\delta^{13}\text{C}$ ($-3.3 \pm 3.1\text{‰}$) and $\delta^{18}\text{O}$ ($-4.0 \pm 1.5\text{‰}$) means. Similar to zebra, many taxa, such as waterbuck ($n = 13$; $-0.8 \pm 2.4\text{‰}$), bushpig (*Potamochoerus* sp.; $n = 9$; $-7.8 \pm 5.1\text{‰}$), and bush duiker ($n = 6$; $-11.2 \pm 3.2\text{‰}$), had quite variable $\delta^{13}\text{C}$ values (Table 6). This variability may suggest that there are important changes in $\delta^{13}\text{C}$ values through time at Kalemba. $\delta^{18}\text{O}$ values, as can be seen for zebra, were not as variable as $\delta^{13}\text{C}$ values, but the fact that $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are known to co-vary warrants an investigation of $\delta^{18}\text{O}$ values through time as well.

There are three potential levels at which changes in $\delta^{13}\text{C}$ and/or $\delta^{18}\text{O}$ values can be investigated at Kalembe: the excavation level, the horizon, and the occupational unit. Sample sizes for the 47 individual excavation levels are not large enough for statistical testing. Using the 13 individual horizons, Kruskal-Wallis tests failed to find any significant differences for browsers ($n = 11$; $\delta^{13}\text{C}$: $p = 0.936$; $\delta^{18}\text{O}$: $p = 0.570$) or fresh grass grazers ($n = 17$; $\delta^{13}\text{C}$: $p = 0.270$; $\delta^{18}\text{O} = 0.213$). For grazers ($n = 49$), however, a significant difference was found in $\delta^{18}\text{O}$ values ($p = 0.002$). No difference was found for $\delta^{13}\text{C}$ values ($p = 0.363$). Kruskal-Wallis tests for zebra confirmed the significant difference in $\delta^{18}\text{O}$ values ($p = 0.008$) and the lack of a significant difference in $\delta^{13}\text{C}$ values ($p = 0.263$). For grazers generally, and zebra specifically, $\delta^{18}\text{O}$ values became higher over time, suggesting greater aridity.

Phillipson (1973, 1976) further grouped the horizons into occupational units. As with the horizons, browsers ($\delta^{13}\text{C}$: $p = 0.809$; $\delta^{18}\text{O}$: 0.404) and fresh grass grazers ($\delta^{13}\text{C}$: $p = 0.055$; $\delta^{18}\text{O}$: $p = 0.536$) did not show any significant differences between analytical units (Figure 4A, B). There was, however, statistical support for a difference in $\delta^{18}\text{O}$ values for grazers ($p = 0.034$). The confidence intervals (CIs) (MSA-LSA transition: -4.6‰ to -3.8‰; LSA: -5.0‰ to -2.7‰; late LSA: -2.9‰ to -0.3‰) indicated a trend towards higher $\delta^{18}\text{O}$ values over time (Table 7; Figure 4A). No support was found for a difference in $\delta^{13}\text{C}$ values ($p = 0.091$) for grazers, but the CIs (MSA-LSA transition: -3.5‰ to -1.7‰; LSA: -4.1‰ to -1.2‰; late LSA: -9.7‰ to -2.5‰) suggested that there may be some sort of temporal pattern (Figure 4B). The Kruskal-Wallis test was rerun after dropping the MSA occupational unit (which is represented by a single zebra sample). Under this testing condition both $\delta^{13}\text{C}$ ($p = 0.042$) and $\delta^{18}\text{O}$ values ($p = 0.024$) were found to have significant differences for grazers (Table 7). A series of Mann-Whitney U tests were run to explore which occupational unit or units may be driving this difference. From these

analyses it is clear that the MSA-LSA transition unit had significantly higher $\delta^{13}\text{C}$ values ($p = 0.011$) and lower $\delta^{18}\text{O}$ values ($p = 0.004$) than the late LSA unit. The Mann-Whitney U tests failed to find any significant differences in $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ values between the MSA-LSA transition and LSA units ($\delta^{13}\text{C}$: $p = 0.536$; $\delta^{18}\text{O}$: $p = 0.451$) or the LSA and late LSA units ($\delta^{13}\text{C}$: $p = 0.067$; $\delta^{18}\text{O}$: $p = 0.114$).

Similar trends across occupational units were also investigated in the zebra sample. Again, $\delta^{18}\text{O}$ values were found to be significantly different whether the single sample from the MSA is included ($p = 0.013$) or not ($p = 0.008$), but $\delta^{13}\text{C}$ values were significantly different only if the MSA sample is excluded ($p = 0.085$ v. $p = 0.040$). The slightly overlapping CIs for $\delta^{18}\text{O}$ values (MSA-LSA transition: -4.8‰ to -4.0‰; LSA: -4.0‰ to -2.0‰; late LSA: -2.9‰ to -0.3‰) clearly show that the trend is towards higher values over time (Table 7). As with the grazers generally, Mann-Whitney U tests found the difference between the MSA-LSA transition and the late LSA ($\delta^{13}\text{C}$: $p = 0.008$; $\delta^{18}\text{O}$: $p = 0.003$) to be the primary driver of the change. This can be seen in the CIs, which did not overlap between the MSA-LSA transition and late LSA for either $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ values ($\delta^{13}\text{C}$ CIs: MSA-LSA transition: -3.9‰ to -1.8‰; LSA: -4.9‰ to -1.0‰; late LSA: -9.7‰ to -6.4‰). Based on the CIs, the trend was toward lower $\delta^{13}\text{C}$ values (Table 7). These results are mirrored by the estimates of C_4 consumption for zebra in the occupational units. During the MSA-LSA transition and the LSA, zebra were estimated to have consumed 71% (normal-condition end-members) or 65% (both other sets of end-member assumptions) C_4 biomass. There is no difference in estimated C_4 consumption between the MSA-LSA transition and the LSA. While these values are low, they are not outside the range of variation for modern zebra (Cerling et al., 2015). In the late LSA, however, estimated C_4 consumption by zebra fell to 33% (normal-condition end-members) or 18% (both other sets of

end-member assumptions), well below modern values (Cerling et al., 2015).

Discussion

Both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are systematically lower at Kalembo Rockshelter than at Porc Epic or the Lukenya Hill sites. However, the southeastern African ecosystem within which Kalembo is found is very different from the East African ecosystem of the other two sites. The granite-greenstone bedrocks where Kalembo is located erode into soils with varying fertility and structural properties (Thompson, 1965; Phillipson, 1976; Stagman, 1978). Serpentinite soils, which cover much of the Zambian Highveld, support mostly grasslands and shrubs, as their high levels of nickel, chromium, and copper are toxic to the Miombo woodlands (Vincent et al., 1961; Wild, 1965; Prendergast, 1979). The grasses that grow on these sandy and acidic soils typically have lower palatability and digestibility compared with the grassland savannas found on the more fertile soils derived from volcanic rocks and limestone in Kenya and Ethiopia (Bell, 1982). This soil control on grass ecosystem structure may play a role in the lower $\delta^{13}\text{C}$ values at Kalembo. Precipitation $\delta^{18}\text{O}$ values are also known to differ between southeastern and East Africa. Zambia (Ndola: -5.5‰) is characterized by lower precipitation $\delta^{18}\text{O}$ values than Kenya (Kericho: -2.8‰) or Ethiopia (Addis Ababa: -1.3‰) based on the International Atomic Energy Agency and World Meteorological Organization's (2016) Global Network of Isotopes in Precipitation. These values are consistent with groundwater, speleothem, and ice core data that show inland parts of Africa had lower $\delta^{18}\text{O}$ values for precipitation than areas closer to the coast during the Last Glacial Maximum (Jasechko et al., 2015). The differences in grass biomass and precipitation $\delta^{18}\text{O}$ values between southeastern and East Africa mean that stable isotope values for fossil faunal tooth enamel cannot be directly compared between the study sites. While Porc

897 Epic and Lukenya Hill are more ecologically similar, chronological uncertainty makes a
 898 discussion of trends, instead of specific comparisons, more appropriate.

899 The results from Porc Epic do not support the expectations of lower $\delta^{13}\text{C}$ values and
 900 higher $\delta^{18}\text{O}$ values over time based on the shift from reduncines lower in the sequence to
 901 alcelaphines higher up. While the small sample of mixed feeders appears to have consumed more
 902 C_3 biomass over time, the overall estimated C_4 consumption is similar to that in modern open
 903 environments like the Kalahari and Nairobi (Sponheimer and Lee-Thorp, 2003). The behavioral
 904 evidence for the LSA at Porc Epic is debatable. Pleurdeau (2005) identified 33 backed bladelets
 905 or microlithic geometrics (only nine from the 1974–1976 excavations with secure provenience),
 906 but Leplongeon (2014) argues that none of these was intentionally made. If Porc Epic does
 907 contain an LSA component within its Pleistocene lithic assemblage, the stable isotope results
 908 would support the Tryon and Faith (2016) model that ‘crosscuts’ habitat and environmental
 909 differences. There is little change in local environment and climate over time based on the stable
 910 isotope analysis, and most tools are made on local flint (Pleurdeau, 2001, 2005). Obsidian, which
 911 at Porc Epic may come from up to 200 km away (Negash and Shackley, 2006), is rare and
 912 primarily present in the earlier MSA parts of the assemblage (Pleurdeau, 2001, 2005) as is
 913 suggested in the Tryon and Faith (2016) model.

914 The shift towards increased aridity from the MSA to the LSA at the Lukenya Hill sites is
 915 unexpected based on the stability of the faunal assemblage across sites and through time
 916 (Marean, 1990, 1992). Open and arid environments at Lukenya Hill, especially GvJm-22, GvJm-
 917 62, and GvJm-46, are indicated by the percent of individuals consuming $>70\%$ C_4 biomass. At
 918 $\sim 80\%$ this value is greater than at Lake Turkana and the Serengeti, which are two of the most
 919 open modern ecosystems (Sponheimer and Lee-Thorp, 2003). These estimated levels of C_4

consumption are consistent, however, with the 76% recorded for Rusinga and Mfangano (~100-35 ka) in the Lake Victoria region (Garrett et al., 2015). The estimated consumption of C₄ biomass at GvJm-19 is lower than at Rusinga and Mfangano and the other Lukenya Hill sites, but is similar to modern open environments. The evidence for higher $\delta^{18}\text{O}$ values, indicating more arid conditions in the LSA than the MSA, supports Ambrose's (1998a, 2002) model of the MSA to the LSA transition whereby the LSA is characterized by increased social connectedness and long-distance exchange in an effort to mitigate risk. Kusimba (2001) found the MSA lithic assemblage of GvJm-46 to be dominated by local quartz. The Pleistocene LSA of GvJm-62 contains only rare pieces of non-local chert and obsidian, and the tools made from these non-local sources are quite large (Barut, 1997; Kusimba, 1999). A greater amount of non-local obsidian is found in the GvJm-22 occurrence E LSA assemblage. Chert and obsidian at GvJm-22 were more exhaustively reduced than in the GvJm-62 assemblage (Kusimba, 1999). Kusimba (2001) interpreted this change in lithic raw material use as indicative of greater mobility and increased social connectivity. Combined with the evidence for more arid conditions associated with LSA assemblages at Lukenya Hill presented here, Kusimba's analysis (2001) fits well with Ambrose's (1998b, 2002) risk reduction model. The terminal Pleistocene assemblage from GvJm-19 represents a microlithic industry made primarily on local raw materials. It is possible that GvJm-19 correlates with climate amelioration and a shift in trade whereby social networks became signified by non-lithic material, like the OES beads that are common in the GvJm-19 assemblage (Barut, 1994; Kusimba, 2001). The stable isotope results suggest arid and open conditions during GvJm-19 times, but even if some sort of climate amelioration occurred at this time it would not offer support to the Eren et al. (2013) model since the LSA started much earlier at Lukenya Hill.

943 Expectations for changes in both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ enamel values are met at Kalembe
 944 Rockshelter. The direction of the change in $\delta^{13}\text{C}$ enamel values is towards lower values over
 945 time. While this was the trend expected for a difference between the LSA and the late LSA
 946 occupations, Mann-Whitney U tests did not find any differences between these two time periods.
 947 No difference was found between the MSA-LSA transition and the LSA occupation either. The
 948 $\delta^{13}\text{C}$ enamel values for grazers shift significantly in the direction of lower values, indicating the
 949 inclusion of greater C_3 biomass in diets over time. $\delta^{18}\text{O}$ enamel values become higher over time,
 950 even through the late LSA which was expected to record a shift to lower values from the LSA.
 951 There are two possible explanations, not mutually exclusive, which may explain the dietary shift
 952 seen in grazers. The first possibility is that these results reflect a change in diet towards more C_3
 953 browse, even for zebra. Higher $\delta^{18}\text{O}$ values, representing increased aridity, along with poor soils
 954 and low quality grass biomass, if current conditions can be extrapolated to the past, may have
 955 forced grazers to consume significant amounts of C_3 non-grass. A second explanation, which
 956 cannot be completely ruled out, is a mix of C_3 and C_4 grasslands, especially towards the end of
 957 the LSA and into the late LSA. Lee-Thorp and Beaumont (1995) report values similar to those
 958 from Kalembe for *Equus quagga* at Equus Cave in South Africa where they argue C_3 grasses
 959 existed in the region shortly before ~10 ka. The shift to higher $\delta^{18}\text{O}$ enamel values at Kalembe
 960 could also indicate a shift to cooler growing season temperatures which would be necessary for
 961 the growth of C_3 grasses (Ehleringer et al., 1997). It is possible that C_4 grasses grew on warmer
 962 north-facing slopes and C_3 grasses on cooler south-facing slopes in the Kalembe area, similar to
 963 in the Eastern Cape of South Africa today (Cowling, 1983; Ruwanza and Shackleton, 2015).
 964 While Kalembe may not be far enough south for the same climatic mechanisms that support the
 965 growth of C_3 grasses in the Eastern Cape, definitively differentiating between the two

966 explanations is not possible based only on the stable isotope data presented here.

967 The evidence from Kalemba could support either the Ambrose (1998 a, b, 2002) or Tryon
968 and Faith (2016) models. The environment becomes more arid over time, and animal resources
969 may have become scarcer if the inclusion of C₃ biomass in grazer diets can be an indicator of
970 resource stress. These two factors would support Ambrose's (1998b, 2002) risk reduction model.
971 However, the primary differences in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are between the MSA-LSA transition
972 and the late LSA. Dry and open conditions into the late LSA appear inconsistent with
973 Phillipson's (1980) proposal that LSA microliths were developed to be used as arrowheads in
974 humid forested environs. It is possible, though, that the small sample size from the LSA and the
975 chronological uncertainty of the LSA, with dates that are inverted with the MSA-LSA transition,
976 could be factors in the lack of a significant difference between the LSA and other occupation
977 units at Kalemba. Additionally, there may also have been an environmental difference from the
978 MSA to the MSA-LSA transition, but the small sample size from the MSA precludes such a
979 comparison. On the other hand, Phillipson's (1976) own interpretation of less residential
980 mobility over time, and the fact that the LSA and the late LSA tool industries are made almost
981 exclusively on local raw materials lend support to the Tryon and Faith (2016) model. If there are
982 truly little or no differences in climate and environment between the MSA-LSA transition and
983 the LSA and the LSA and late LSA, then the change in lithic technology may 'crosscut'
984 indicators of environmental change.

985 The preliminary assessment of the three MSA-LSA transition models based on the site-
986 specific data reported here suggests that no single model will be able to provide an explanation
987 for the transition at all sites across Africa. While more support was found in this study for
988 Ambrose's (1998a, 2002) risk reduction model and Tryon and Faith's (2016) non-environmental

model, the climate amelioration model proposed by Eren et al. (2013) may operate at other sites. A combination of characteristics from two models may also be possible. For instance, at Kalembe a shift to more arid conditions, as stipulated in Ambrose's (1998a, b, 2002) model, may have resulted in less residential mobility and more intensive exploitation of local resources, as detailed in the Tryon and Faith (2016) model. It is also possible that the interpretations above may change slightly once the study sites are dated more accurately. Additional breaks in the Porc Epic sequence may be identified, and it may be possible to determine if GvJm-62 and GvJm-46 overlap in time. Plus, the rock fall in Horizon K at Kalembe may not represent an extended occupational hiatus between the MSA-LSA transition and the LSA occupations.

Again, the purpose of this study was not to offer a new model of the MSA-LSA transition or to rigorously test the existing models, but to provide critical site-specific environmental data which were not available through other analytical methods. The results of the stable isotope analysis emphasize the need to develop local, site-level, paleoenvironmental databases for a better understanding of Late Pleistocene ecology. Environmental variability over time at a single site may offer insights to Late Pleistocene biogeography (Marean, 1992; Tryon and Faith, 2013). Small climatic differences within the occupation of a site may be significant for Late Pleistocene human dispersals, migrations, and behavior (Faith et al., 2015; Rowan et al., 2015). The fact that the timing of the transition from the MSA to the LSA varies from region to region and site to site across Africa (Ambrose, 2002; Tryon and Faith, 2013; Wurz, 2013), implies that local environmental and climatic conditions may be at least partially responsible.

Conclusions

Site-specific paleoenvironmental reconstructions based on stable isotope analysis of fossil faunal tooth enamel provided here demonstrate a critical need to think locally in terms of the role of environment and climate in the behavioral transitions which characterized the change from the MSA to the LSA. $\delta^{18}\text{O}$ enamel values of fossil faunal tooth enamel show that sites in Kenya and Zambia become significantly more arid over time. It is likely that forested and wooded environments in Kenya and Zambia retreated leaving more open habitats (Barham, 2000; Tryon and Faith, 2013; Garrett et al., 2015) and revealing migration and mixing corridors for fauna, including humans, which were not present during earlier, more humid, periods (Lorenzen et al., 2012; Faith et al., 2015). Site-specific paleoenvironmental and paleoclimatic contexts provide evidence for the development of new adaptive landscapes (e.g., Kingston, 2007), which played a role in the behavioral changes, migrations, and group interactions of the transition from the MSA to the LSA. The spatial and temporal spread of site-specific paleoenvironmental reconstructions must be increased and individual sites considered as part of integrated social networks in order to continue refining models of Late Pleistocene behavioral, demographic, and social change. Thinking locally has the advantage of characterizing such networks from a “ground-up” approach and using empirical data to test models of behavioral change.

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Figure Captions

Figure 1. Map of Africa (geospatial data from Natural Earth) with break out maps of Zambia, Ethiopia, and Kenya. The approximate locations of Kalemba Rockshelter, Porc Epic, and Lukenya Hill within the appropriate country are each indicated by a yellow star.

Figure 2. Enamel $\delta^{18}\text{O}$ (A) and $\delta^{13}\text{C}$ (B) data for trophic categories at Porc Epic divided into above and below 160 cm units. As can be seen in the scatter plot, samples from above and below 160 cm have overlapping ranges for all trophic categories, which implies little or no change in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values over time. Sample sizes are listed on the Y-axis following the name of the trophic category, with the first number being the sample size for below 160 cm and the second number being the sample size for above 160 cm. See Table 3 for results of the non-parametric statistical tests and confidence intervals.

Figure 3. Box-and-whisker plots of $\delta^{18}\text{O}$ (A) and $\delta^{13}\text{C}$ (B) values overlaid on the raw point data for grazers at Lukenya Hill. These plots include data from all four of the Lukenya Hill sites grouped into the three behavioral units of the Middle Stone Age (MSA), occurrence F (Oc. F), and the Later Stone Age (LSA). While a shift towards higher $\delta^{18}\text{O}$ values is suggested, there is little or no change in $\delta^{13}\text{C}$ values. Sample sizes are in parentheses on the Y-axis following the name of the behavioral unit. Boxes represent the upper and lower quartiles for each behavioral unit. The line within the box represents the median value. Individual data points which are not touched by whiskers are outliers calculated as $1.5 \times \text{IQR}$ (inter-quartile range) in SPSS. See Table 5 for results of the non-parametric statistical tests and confidence intervals.

1686 Figure 4. Box-and-whisker plots of enamel $\delta^{18}\text{O}$ (A) and $\delta^{13}\text{C}$ (B) data for grazers, fresh grass
1687 grazers, and browsers at Kalembe Rockshelter divided into the four occupational units. Both
1688 $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ enamel values change over time, particularly for grazers. $\delta^{18}\text{O}$ values become
1689 higher over time and $\delta^{13}\text{C}$ values become lower. Sample sizes are listed in chronological order
1690 on the Y-axis following the name of the trophic category, with the first number being the late
1691 LSA sample size and the last number being the MSA sample size. Boxes represent the upper and
1692 lower quartiles for each trophic category. The line within the box represents the median value.
1693 Stars represent outliers calculated as $1.5 \times \text{IQR}$ (inter-quartile range) in SPSS. Circles are used
1694 when a trophic category is represented by a single sample for an occupational unit. See Table 7
1695 for significant differences and confidence intervals.

B

Mixed Feeders (2/13)

▽ Below 160 cmbs

 $\delta^{18}\text{O}$ tooth enamel (‰)

←
Less Arid

→
More Arid

 $\delta^{13}\text{C}$ tooth enamel (‰)

← More C₃

More C₄

Grazers (4/6/38/1)

Fresh Grass Grazers (-/7/10/-)

Browsers (1/6/3/1)

Table 1. Summary of approximate age ranges, archaeological highlights, and taxa sampled for the study sites.

Site (<i>n</i>)	Age in years BP	Taxon (<i>n</i>)	Common Name	Archaeology
Porc Epic (60)	~ 100 – 40 ka	<i>Aepyceros melampus</i> (3)	Impala	Three Pleistocene aged MSA
		<i>Damaliscus lunatus</i> (3)	Tsessebe	units and one Holocene aged
		<i>Nanger granti</i> (2)	Grant’s gazelle	LSA unit. Only the MSA units
		<i>Madoqua guentheri</i> (1)	Gunther’s dik-dik	are sampled in this study. At
		<i>Syncerus caffer</i> (9)	African buffalo	~160 cm below the surface
		<i>Syncerus antiquus</i> (5)	---	backed pieces and microliths,
		<i>Oryx beisa</i> (1)	East African oryx	while rare, begin to appear and
		<i>Neotragus</i> sp. (1)	---	may represent the earliest LSA
		<i>Raphicerus</i> sp. (1)	---	at Porc Epic. At this possible
		<i>Kobus ellipsiprymnus</i> (3)	Waterbuck	LSA level there is also a shift
		<i>Redunca redunca</i> (6)	Bohor reedbuck	in the faunal assemblage from
		<i>Tragelaphus strepsiceros</i> (5)	Greater kudu	a dominance of fresh grass
		<i>Tragelaphus</i> sp. (2)	---	feeding reduncines to more dry
		<i>Phacochoerus</i> sp. (12)	Warthog	grass feeding alcelaphines.

		<i>Potamochoerus</i> sp. (1)	Bushpig	
		<i>Equus quagga</i> (4)	Plains zebra	
		<i>Equus grevyi</i> (1)	Grevy's zebra	
Lukenya Hill (89)				
GvJm-22 (46)				
Occurrence E (25)	> 46 – 15 ka	<i>Alcelaphus buselaphus</i> (3)	Hartebeest	LSA assemblage with
		<i>Connochaetes taurinus</i> (3)	Blue wildebeest	abundant backed pieces and
		<i>Damaliscus hypsodon</i> (11)	---	retouched tools
		<i>Nanger granti</i> (1)	Grant's gazelle	
		<i>Eudorcas thomsonii</i> (1)	Thomson's gazelle	
		<i>Redunca fulvorufula</i> (1)	Mountain reedbuck	
		<i>Tragelaphus oryx</i> (1)	Eland	
		<i>Phacochoerus</i> sp. (1)	Warthog	
		<i>Potamochoerus</i> sp. (1)	Bushpig	
		<i>Equus quagga</i> (2)	Plains zebra	
Occurrence F/G (21)	> 46 – 26 ka	<i>Alcelaphus buselaphus</i> (4)	Hartebeest	Mixed MSA and LSA artifacts.

		<i>Connochaetes taurinus</i> (1)	Blue wildebeest	Predominantly Levallois
		<i>Damaliscus hypsodon</i> (8)	---	technology.
		<i>Eudorcas thomsonii</i> (1)	Thomson's gazelle	
		<i>Oryx beisa</i> (1)	East African oryx	
		<i>Ourebia ourebi</i> (1)	Oribi	
		<i>Tragelaphus oryx</i> (1)	Eland	
		<i>Equus quagga</i> (4)	Plains zebra	
GvJm-62 (15)	> 30 – 25 ka	<i>Alcelaphus buselaphus</i> (4)	Hartebeest	Terminal Pleistocene and
		<i>Connochaetes taurinus</i> (1)	Blue wildebeest	Pleistocene LSA assemblages.
		<i>Damaliscus hypsodon</i> (5)	---	Only the Pleistocene sampled
		<i>Eudorcas thomsonii</i> (1)	Thomson's gazelle	here. Microliths rare in the
		<i>Equus quagga</i> (4)	Plains zebra	Pleistocene LSA (~12%).
GvJm-19 (11)	~ 14 ka	<i>Alcelaphus buselaphus</i> (3)	Hartebeest	Terminal Pleistocene LSA unit
		<i>Connochaetes taurinus</i> (2)	Blue wildebeest	with curved crescents, backed
		<i>Damaliscus hypsodon</i> (1)	---	blades, and microliths.
		<i>Sylvicapra grimmia</i> (1)	Bush duiker	Holocene aceramic and

		<i>Ourebia ourebi</i> (1)	Oribi	ceramic units also present.
		<i>Redunca fulvorufula</i> (1)	Mountain reedbuck	Only the terminal Pleistocene
		<i>Phacochoerus</i> sp. (1)	Warthog	LSA sampled here.
		<i>Equus quagga</i> (1)	Plains zebra	
GvJm-46 (17)	> 40 ka	<i>Damaliscus hypsodon</i> (15)	---	MSA and LSA units separated
		<i>Eudorcas thomsonii</i> (1)	Thomson's gazelle	by rock fall. Only the MSA
		<i>Equus quagga</i> (1)	Plains zebra	sampled here.
Kalembe Rockshelter (88)	> 40 – 8 ka	<i>Connochaetes taurinus</i> (9)	Blue wildebeest	Four occupational units
		<i>Eudorcas thomsonii</i> (1)	Thomson's gazelle	identified based on lithic
		<i>Sylvicapra grimmia</i> (6)	Bush duiker	technology: MSA, MSA-LSA
		<i>Hippotragus niger</i> (1)	Sable antelope	transition, LSA 'Nachikufan I,'
		<i>Ourebia ourebi</i> (1)	Oribi	and late LSA Makwe Industry.
		<i>Kobus ellipsiprymnus</i> (13)	Waterbuck	Two occupational hiatuses
		<i>Redunca arundinum</i> (4)	Southern reedbuck	inferred: one between MSA
		<i>Tragelaphus oryx</i> (4)	Eland	and MSA-LSA transition and
		<i>Tragelaphus scriptus</i> (1)	Bushbuck	the other between MSA-LSA

<i>Phacochoerus</i> sp. (5)	Warthog	transition and the LSA. All
<i>Potamochoerus</i> sp. (9)	Bushpig	occupation units sampled.
<i>Equus quagga</i> (34)	Plains zebra	

Table 2. Porc Epic Cave enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ means $\pm$ standard deviations, 95% confidence intervals (CI) and average estimated percent C_4 consumption by taxon.

Taxon (<i>n</i>)	$\delta^{13}\text{C}$	95% CI	$\delta^{18}\text{O}$	95% CI	%C ₄ ^a		
					N	WS	A
Grazers							
<i>Damaliscus lunatus</i> (3)	0.0±1.8	-2.1 to 1.0	1.7±1.6	0.1 to 3.3	90	88	90
<i>Equus quagga/grevyi</i> (5)	-2.2±1.3	-3.5 to -1.0	2.3±1.6	0.9 to 3.9	76	70	72
<i>Phacochoerus</i> sp. (13)	-3.6±3.0	-5.5 to -2.1	1.5±2.1	0.4 to 2.7	66	58	59
Fresh Grass Grazers							
<i>Kobus ellipsiprymnus</i> (3)	-1.7±1.6	-3.0 to 0.1	0.5±3.6	-3.7 to 2.8	79	74	76
<i>Redunca redunca</i> (5)	-1.8±2.3	-4.3 to 0.2	0.6±1.2	-0.6 to 1.6	78	73	75
<i>Syncerus caffer</i> (9)	-0.7±3.0	-2.9 to 1.1	0.7±2.0	-0.6 to 2.0	86	82	84
Mixed Feeders							
<i>Syncerus antiquus</i> (5)	-6.5±1.2	-7.5 to -5.3	3.5±3.3	0.2 to 6.0	47	34	35
<i>Aepyceros melampus</i> (3)	-3.3±1.6	-5.0 to -1.9	2.1±2.7	-0.3 to 5.0	68	61	62
<i>Nanger granti</i> (2)	-3.8±1.2	-4.6 to -2.9	3.2±0.4	2.9 to 3.5	65	57	58
<i>Tragelaphus strepsiceros</i> (7)	-6.5±2.7	-8.3 to -4.2	2.6±2.0	1.0 to 4.1	46	33	34

^aN = normal-conditions end-members; WS = water-stressed C₃ end-member; A = C₃ and C₄ arid end-members.

Table 3. Results (*p*-values) of non-parametric tests and 95% confidence intervals (CI) of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel values for Porc Epic Cave based on splitting the archaeological sequence into two units at 160 cm below surface as described in the text.

Trophic Category	$\delta^{13}\text{C}$			$\delta^{18}\text{O}$		
	<i>p</i> -value	60-160 95% CI (<i>n</i>)	160-300 95% CI (<i>n</i>)	<i>p</i> -value	60-160 95% CI (<i>n</i>)	160-300 95% CI (<i>n</i>)
Grazers	0.329	-4.7 to -1.8 (16)	-2.8 to -0.2 (6)	0.154	0.9 to 3.0 (16)	0.0 to 1.5 (6)
Fresh Grass Grazers	0.799	-2.9 to 0.3 (12)	-3.4 to 0.9 (5)	0.328	-1.0 to 1.5 (12)	0.5 to 2.6 (5)
Mixed Feeders	0.476	-6.6 to -4.4 (13)	-8.9 to -5.0 (2)	0.076	1.6 to 4.1 (13)	5.0 to 5.2 (2)

Table 4. Enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ means, standard deviations, 95% confidence intervals (CI) and average estimated percent C_4 consumption by Lukenya Hill grazers.

Taxon (<i>n</i>)	$\delta^{13}\text{C}$	95% CI	$\delta^{18}\text{O}$	95% CI	%C ₄ ^a		
					N	WS	A
GvJm-22 Trench C and C+ balk							
<i>Alcelaphus buselaphus</i> (4)	-0.1±1.4	-2.1 to 1.0	-3.2±1.4	-4.6 to -1.3	90	88	90
<i>Connochaetes taurinus</i> (4)	0.3±0.9	-0.5 to 1.6	-1.2±1.9	-2.9 to 1.5	93	91	93
<i>Damaliscus hypsodon</i> (14)	-0.2±1.0	-0.6 to 0.4	-1.9±1.5	-2.7 to -1.2	89	87	89
<i>Equus quagga</i> (6)	-1.5±1.6	-2.9 to -0.2	-2.5±1.7	-3.9 to -1.1	80	75	77
GvJm-62							
<i>Alcelaphus buselaphus</i> (4)	0.1±1.5	-1.8 to 1.4	-4.7±1.0	-5.7 to -3.5	91	89	92
<i>Damaliscus hypsodon</i> (5)	0.6±0.4	0.2 to 0.9	-3.9±1.0	-4.6 to -3.0	94	93	95
<i>Equus quagga</i> (4)	-2.6±1.2	-4.1 to -1.4	-2.7±0.8	-3.5 to -1.9	73	67	69
GvJm-19							
<i>Alcelaphus buselaphus</i> (3)	-1.6±0.8	-2.3 to -0.7	-2.8±1.1	-4.0 to -1.9	79	75	76
<i>Connochaetes taurinus</i> (2)	-0.3±0.6	-0.7 to 0.2	-3.2±0.0	---*	89	86	88
GvJm-46							
<i>Damaliscus hypsodon</i> (15)	0.7±1.0	0.2 to 1.2	-3.7±1.1	-4.2 to -3.2	94	96	97

^aN = normal-conditions end-members; WS = water-stressed C_3 end-member; A = C_3 and C_4 arid end-members

*Note that both $\delta^{18}\text{O}$ values for *Connochaetes taurinus* are -3.2‰ so no CI is reported.

Table 5. Results (p -values) of non-parametric tests and 95% confidence intervals (CIs) of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel values for *D. hypsodon* and grazers at Lukenya Hill under two conditions: Middle Stone Age (MSA) versus Later Stone Age (LSA) assemblages; MSA versus Occurrence F versus LSA assemblages.^a

MSA versus LSA		95% CIs (n)	MSA versus F versus LSA	95% CIs (n)
<i>D. hypsodon</i>				
$\delta^{13}\text{C}$	0.101	MSA: 0.0 to 1.0 (23) LSA: -0.3 to 0.5 (17)	0.086	MSA: 0.2 to 1.2 (15) F: -1.0 to 1.1 (8) LSA: -0.3 to 0.5 (17)
$\delta^{18}\text{O}$	0.014	MSA: -3.8 to -2.8 (23) LSA: -2.7 to -1.2 (17)	0.016	MSA: -4.2 to -3.1 (15) F: -3.6 to -1.7 (8) LSA: -2.7 to -1.2 (17)
Grazers				
$\delta^{13}\text{C}$	0.136	MSA: -0.6 to 0.5 (36) LSA: -0.8 to -0.1 (40)	0.067	MSA: -0.5 to 0.9 (19) F: -1.4 to 0.3 (18) LSA: -0.8 to -0.1 (39)
$\delta^{18}\text{O}$	0.049	MSA: -3.5 to -2.6 (36) LSA: -2.7 to -1.7 (40)	0.046	MSA: -4.0 to -2.8 (19) F: -3.3 to -1.9 (18) LSA: -2.7 to -1.7 (39)

^aBold indicates significance at the $p < 0.05$ level.

Table 6. Kalembe Rockshelter enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ means, standard deviations, 95% confidence intervals (CI) and average estimated percent C_4 consumption by taxon.

Taxon (<i>n</i>)	$\delta^{13}\text{C}$	95% CI	$\delta^{18}\text{O}$	95% CI	%C ₄ ^a		
					N	WS	A
Grazers							
<i>Connochaetes taurinus</i> (9)	-0.7±1.7	-2.0 to 0.2	-3.7±1.6	-4.7 to -2.6	86	82	84
<i>Equus quagga</i> (34)	-3.3±3.1	-4.3 to -2.3	-4.0±1.5	-4.4 to -3.4	68	61	62
<i>Phacochoerus</i> sp. (5)	-4.6±2.6	-7.1 to -2.2	-4.2±1.4	-5.5 to -2.8	59	49	51
Fresh Grass Grazers							
<i>Kobus ellipsiprymnus</i> (13)	-0.8±2.4	-2.3 to 0.2	-4.7±1.2	-5.3 to -4.0	85	81	83
<i>Redunca arundinum</i> (4)	-2.2±5.4	-10.1 to 1.8	-1.8±1.8	-4.4 to -0.1	76	70	72
Browsers							
<i>Sylvicapra grimmia</i> (6)	-11.2±3.2	-13.6 to -8.4	-4.4±1.6	-5.7 to -3.1	14	0	0
<i>Tragelaphus oryx</i> (4)	-10.6±5.6	-14.7 to -2.3	-4.6±2.7	-7.4 to -1.2	19	0	0
Omnivores							
<i>Potamochoerus</i> sp. (9)	-7.8±5.1	-11.0 to -4.3	-5.0±2.4	-6.6 to -3.4	38	23	24

^aN = normal-conditions end-members; WS = water-stressed C₃ end-member; A = C₃ and C₄ arid end-members

Table 7. Results (p -values) of non-parametric tests and 95% confidence intervals (CIs) of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel values for Kalembe Rockshelter based on occupation units.^a

	With MSA	Without MSA	95% CIs (n)
<i>E. quagga</i>			
$\delta^{13}\text{C}$	0.085	0.040	MSA-LSA transition: -3.9 to -1.8 (27)
			LSA: -4.9 to -1.0 (3)
			Late LSA: -9.7 to -6.4 (3)
$\delta^{18}\text{O}$	0.013	0.008	MSA-LSA transition: -4.8 to -4.0 (27)
			LSA: -4.0 to -2.0 (3)
			Late LSA: -2.9 to -0.3 (3)
Grazers			
$\delta^{13}\text{C}$	0.091	0.042	MSA-LSA transition: -3.5 to -1.7 (38)
			LSA: -4.1 to -1.2 (6)
			Late LSA: -9.7 to -2.5 (4)
$\delta^{18}\text{O}$	0.034	0.024	MSA-LSA transition: -4.6 to -3.8 (38)
			LSA: -5.0 to -2.7 (6)
			Late LSA: -2.9 to -0.3 (4)
Fresh Grass Grazers ^b			
$\delta^{13}\text{C}$	---	0.055	MSA-LSA transition: -2.8 to 0.7 (10)
			LSA: -5.2 to -0.2 (7)
$\delta^{18}\text{O}$	---	0.536	MSA-LSA transition: -5.2 to -3.3 (10)
			LSA: -5.1 to -1.9 (7)

Browsers				
$\delta^{13}\text{C}$	0.809	0.683	MSA-LSA transition: -13.8 to -2.3 (3)	
			LSA: -14.1 to -8.9 (6)	
			Late LSA: -10.9 (1)	
$\delta^{18}\text{O}$	0.404	0.283	MSA-LSA transition: -6.4 to -1.2 (3)	
			LSA: -5.6 to -3.1 (6)	
			Late LSA: -0.7 (1)	

^aBold indicates significance at the $p < 0.05$ level.

^bNote that there are no fresh grass grazer samples from the late LSA occupation unit.